THE ATTAINMENT OF HOMOZYGOSITY IN INBRED STRAINS OF MAIZE

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INTRODUCTION

Six generations of continuous self-fertilization in the naturally cross-fertilized maize plant has been found to be usually sufficient to bring about a rather high degree of homozygosity. Plants which are vigorous, but highly variable at the start, become uniform and constant and markedly reduced in size and in the rapidity of growth when self-fertilized at random. When single plants are used as the progenitors of each successive inbred generation everything depends upon the constitution of these progenitors as to the results obtained. If there is extensive selection for vigorous individuals reduction in heterozygosity may be delayed. Differences in the rate at which homozygosity is approached are expected in different lines, but on the average, without selection, the decrease in heterozygosity theoretically follows the rule of halving the remaining differences in each generation until complete homozygosity is attained. Actual results agree fairly well with this expectation as has been shown previously and by results to be reported here.

After seven generations of self-fertilization a number of strains were tested for homozygosity, as reported in 1918, by comparing progenies from self-fertilized plants with those from intercrossed plants within the same strain (JONES 1918). On the average the crossed plants gave a slight increase in all characters measured. In some strains the increases were statistically significant, whereas, in other strains equally large decreases resulted from crossing, indicating that the test was greatly affected

by environmental influences. On the whole, any increase in size and vigor was slight when compared with the result of crossing unrelated strains.

Some of these same strains have now been brought to the seventeenth generation of self-fertilization. Originally all of the common types of maize were inbred, but only four of the original strains have been continued after the tenth generation and these have descended from a single variety, a yellow dent type known as Leaming.

In the eighth or ninth generations of self-fertilization each of these four strains was separated into two lines which have been continued to the present time. The behavior of these paired lines, continued seven or more generations after separation, gives an indication as to what extent homozygosity had been attained at the time of separation.

For convenience these four strains are now lettered A, B, C and D, the two paired lines within each strain being designated A_1, A_2, B_1, B_2, etc. The generations have not been kept alike in all of the strains on account of the failure to secure self-pollinated seed in some years. The pedigrees of these strains are given in table 1. The first number in each pedigree

TABLE 1

Pedigree relationship of four inbred strains of maize, each separated in the eighth or ninth generation and further self-fertilized from seven to nine generations.

STRAIN DESIGNATION	PEDIGREE NUMBER OF THE PROGENITOR IN EACH GENERATION																	GENERATION WHEN	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Separated	Crossed
A_1	1	9	1	2	4	6	7	5	3	2	1	1	1	1	1	1			8	14
A_2	"	"	"	"	"	"	"	"	6	2	1	1	1	1	1	1	1		8	15
B_1	1	7	1	1	1	4	7	5	4	7	1	1	1	1	1	1	1	1	9	16
B_2	"	"	"	"	"	"	"	"	"	5	2	1	1	4	1	1	1	1	9	16
C_1	"	"	"	2	2	9	2	1	1	4	3	1	1	1	1	1	1	1	9	16
C_2	"	"	"	"	"	"	"	"	"	1	1	1	1	1	1	1	1	1	9	16
D_1	1	6	1	3	4	4	4	2	4	4	2	1	1	1	1	1	1	1	8	16
D_2	"	"	"	"	"	"	"	"	5	5	2	1	1	1	1	1	1		8	15

designates the variety, seed of which grew the first plants to be self-fertilized. Following that, each single plant progenitor is given a number in each generation. It will be noted that the four strains came from three original plants numbered 6, 7 and 9. One strain was separated in the third generation. The two resulting strains are nearly as different as the other strains from separate plants at the start so that they can be con-

sidered as distinct strains. This shows that after two generations of self-fertilization a high degree of heterozygosity still remained, as would be expected.

HOMOZYGOSITY AFTER EIGHT GENERATIONS

Three of the paired strains, A, B and C, have remained visibly alike in the seven to nine generations they have been grown since separation. No consistent differences in general size, habit of growth, time of flowering, details of structure or disease infection can be seen in the field. However, the seeds of C_2 are appreciably brighter in color than those of C_1 although this difference is not clearly apparent every year. In the case of D_1 and D_2, differences were apparent soon after they were separated and they have remained diverse up to the present time. The stalks of D_2 are larger, the leaves are wider and lighter in color. The ears are larger and the seeds are wider and duller in color. These differences are easily apparent during the growing season and at harvest time.

In table 2 the paired strains are compared statistically in height of plant, number of nodes, length of ear and in yield. These figures are

TABLE 2

A comparison of inbred strains of maize from the same sources, but separated after seven generations or more of self-fertilization.

	HEIGHT INCHES	NODES NUMBER	LENGTH OF EAR CENTIMETERS	YIELD IN BUSHELS PER ACRE
A_1	60.8± .47	13.98± .074	10.28± .15	9.4
A_2	61.5± .39	14.25± .079	12.06± .11	17.6
Difference	.7± .61	.27± .108	1.78± .19	8.2
Diff.÷P.E.	1.1	2.5	9.4	
B_1	77.3± .45	13.37± .066	8.64± .13	28.2
B_2	78.3± .66	14.12± .056	8.75± .12	27.3
Difference	1.0± .80	.75± .086	.11± .18	.9
Diff.÷P.E.	1.3	8.7	.6	
C_1	74.7± .60	15.43± .068	11.16± .24	17.0
C_2	73.1± .52	16.02± .063	10.09± .24	16.7
Difference	1.6± .79	.59± .093	1.07± .34	.3
Diff.÷P.E.	2.0	6.3	3.2	
D_1	75.0± .60	14.91± .090	9.96± .16	19.8
D_2	70.8± .63	13.63± .098	13.71± .25	23.7
Difference	4.2± .87	1.28± .133	3.75± .30	3.9
Diff.÷P.E.	4.8	9.6	12.5	

based on duplicate plots of each pair grown close together and representing a total of about 50 plants in each line. All of the paired lines are significantly different in some character but the D lines differ significantly in all characters measured.

The paired lines, after being separated for six or more generations, were crossed both ways and compared with their parental strains. If differences existed when the paired lines were separated, these differences should persist and might result in an increase in growth whenever they were crossed. In table 3 the average of the reciprocal crosses, each grown in duplicate plots, is compared with the average of the two parents, in height, number of nodes, length of ear and yield of grain.

TABLE 3

A comparison of inbred strains of maize from the same source, with their reciprocal intercrosses.

		HEIGHT INCHES	NODES NUMBER	LENGTH OF EAR CENTIMETERS	YIELD IN BUSHELS PER ACRE
A	Parents	61.2±.30	14.1±.05	11.2±.11	13.5
	Hybrids	63.7±.29	14.5±.05	11.6±.08	15.8
	Difference	2.5±.42	.4±.07	.4±.14	2.3
	Diff.÷P.E.	6.0	5.7	2.9	Odds=7:1
B	Parents	77.8±.40	13.7±.06	8.7±.09	27.8
	Hybrids	80.6±.30	13.8±.04	9.2±.09	33.4
	Difference	2.8±.51	.1±.08	.5±.13	5.6
	Diff.÷P.E.	5.5	1.2	3.9	Odds= 158:1
C	Parents	73.8±.40	15.8±.05	10.6±.18	16.8
	Hybrids	72.2±.48	15.8±.05	11.9±.14	25.4
	Difference	−1.6±.62	0±.07	1.3±.23	8.6
	Diff.÷P.E.	2.6	0	5.7	Odds= 144:1
D	Parents	73.0±.46	14.3±.08	11.7±.20	21.8
	Hybrids	80.8±.40	14.7±.06	13.4±.15	38.2
	Difference	7.8±.61	.4±.10	1.7±.25	16.4
	Diff.÷P.E.	12.8	4.0	6.8	Odds= 78:1

The probable error for height, number of nodes and length are calculated from the usual formula for the spread of a frequency distribution. Since yield is based only on the average results of paired plots grown in different parts of the field the significance of the differences is calculated from the method (STUDENT 1908, LOVE 1923) which gives the odds

against such a difference occurring in repeated experiments. These odds are given in table 3 and the increases in yield of the reciprocal crosses over their seed parents are surely significant in all cases except for the A lines.

Wherever there is a significant difference it is an increase of the hybrids over their parents. The crosses in strains A, B and C, do not show a significant increase in all characters measured, so that the differences between the paired lines in each strain are presumably small. In these strains, it will be recalled, no visible differences in size or form could be seen. In the D strain, where noticeable differences existed in the paired lines, the hybrids exceed their parents in all characters measured, by a significant amount. The production of grain is nearly doubled. Height of plant and length of ear are augmented by over 10 percent.

Since the two D lines were different from the time they were separated in the eighth generation, there is no question but that their common ancestor in the seventh generation was still heterozygous. Whether or not all the differences can be attributed to delayed segregation can not be positively stated. There is the possibility based upon direct evidence that germinal changes have occurred in all of the strains, making them different is some degree even when no external differences are apparent.

HOMOZYGOSITY AFTER FOURTEEN GENERATIONS

With the evidence that the strains were not reduced to complete homozygosity by eight generations of self-fertilization the question arises as to how nearly they have approached this condition in later generations. This was tested in the following way. Two different strains, A and B, in which the paired lines did not differ visibly, were crossed in the fourteenth generation for the A strain and the fifteenth generation for the B strain. The F_1 plants of A×B were remarkably uniform and vigorous. Several F_1 plants were self-fertilized and an equal number of plants was pollinated by other plants of the same lot. If the parental strains were not homozygous the F_1 plants would therefore not be all alike and intercrossing these somewhat diverse individuals would not cause as great a reduction in growth the following generation as self-pollinating them. On the other hand if the parental strains were completely homozygous the F_1 plants would all be exactly alike in germinal construction and cross-fertilization among the hybrid offspring would give no different result than self-pollination. This test for homozygosity was first applied by SHULL (1909, 1911) to inbred strains of maize self-fertilized four generations. He found that the F_1 plants intercrossed gave an increase of 13 percent

in production of grain, indicating that the parental strains were not completely homozygous.

The seed ears from the (A×B) F_1 plants, self-fertilized and intercrossed, were equally well developed. The seed of several ears of each lot was mixed and the two lots were planted in alternate rows, replicated three times with guard rows on the outside. Enough seed was planted and the extra plants thinned out to insure a practically perfect stand of plants. The F_1 plants self-pollinated gave a progeny which averaged $76.2 \pm .57$ inches in height compared with $73.8 \pm .70$ for the F_1 plants intercrossed, a difference of $2.4 \pm .90$ in favor of the self-pollinated plants. In yield the results were, respectively, 22.2 ± 1.2 and 22.0 ± 2.4 bushels per acre, a difference less than the probable error of the difference.[1] Since there was no significant difference in height or production of grain, the two characters which are most influenced by heterosis, the two parental strains are apparently each homozygous, as far as this test shows, for all factors which have a measurable effect upon growth.

MUTATIONS IN INBRED STRAINS OF MAIZE

Two new characters have appeared in these four longest-inbred strains, in such a way as to leave little doubt that they are germinal changes and not due to delayed segregation. Since inbred strains of maize, after the first several generations, are uniform in type and much reduced in vigor, changes occurring in any part of the plants are easily noted. Moreover, they can be clearly distinguished from alterations due to out-crossing. Crossing with any plants outside the strain results immediately in an enormous increase in size and rapidity of growth and change in form so that any out-cross is at once noted. Both of the mutational changes in these inbred strains occurred without the plants increasing in vigor or changing in type other than in the character affected.

In 1921 the D_2 strain was in the thirteenth generation of self-fertilization. Three self-pollinated ears were obtained and one of these was clearly segregating for a lethal factor which produced poorly developed, shrunken, light-colored, opaque seeds scattered throughout the ear as shown in figure 1. Heritable characters of this kind, described as defective seeds, have been found to occur quite commonly in all kinds of maize. They were first noticed in 1918 in other inbred strains three years before they were found in the old inbred strains. Since variations of this kind

[1] The triplicate plots were grown in one place and the probable error of yield is here calculated from BESSEL's formula, $E_A = .6745\sqrt{\frac{\Sigma d^2}{n(n-1)}}$ (see LOVE 1923).

were being actively looked for it is very improbable that they could have been occurring in this strain each year and overlooked. It happens that the year before, all of the plants of this particular strain were hand-pollinated, some 15 to 20 plants in each of the paired lines, D_1 and D_2, and if this character were present in the stock it would surely have been noted.

Defective seeds have reappeared in this mutant line every year since, now three generations in succession, and segregating plants out-crossed to

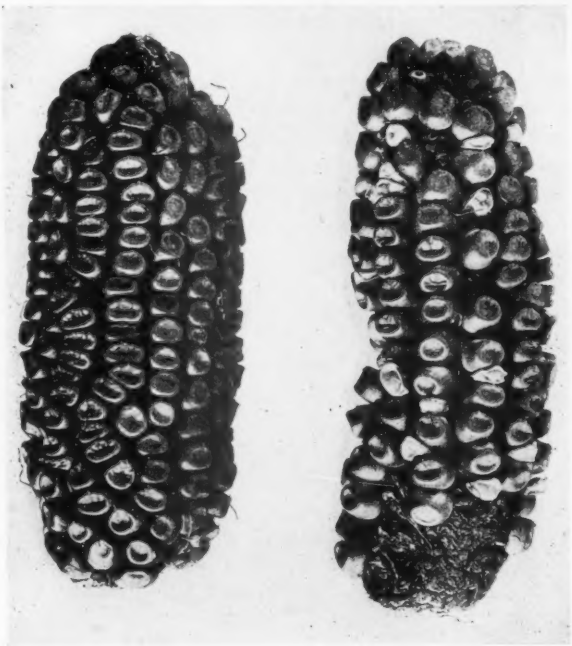


FIGURE 1.—A germinal change which occurred in the thirteenth generation of self-fertilization. The ear on the right is segregating for a lethal factor that produces defective seeds; on the left is a normal ear from the same progeny.

unrelated plants not segregating gave the same type of defectiveness in the second seed generation so that there is clear evidence that the lethal factor is recent in its expression and is heritable.

In 1922 about one-thousand plants of one of the C strains, after more than ten generations of self-fertilization, were grown in an isolated field and detasseled to produce seed crossed by another inbred strain. At

harvest four ears were found with light-red cobs. This strain has always had only pure white cobs and these are characteristically flattened. The ears and plants of this strain are easily identified and are quite distinct from all other inbred strains. The four plants which produced the colored cobs were noted at harvest as being typical for the strain and the ears themselves were no different from the others of the same lot except in the color of the cob. The change therefore can not have been due to out-crossing.

The seeds produced on these aberrant ears were all crossed with a red-cobbed strain before they were found, so that the next-generation plants would have colored cobs in all cases. As yet it has not been possible to test out the new character to determine its inheritance. If it is the same factor as the one that commonly produces red cobs the change has been from a recessive to a dominant condition.

Two other changes have occurred in other inbred strains of maize such that they have every evidence of being recent germinal alterations. One strain, after five generations of self-fertilization, produced, for the first time, striped and variegated plants which occurred regularly thereafter in about 25 percent of the offspring from normal plants. Another strain, after nine generations, gave small, narrow-leaved dwarf plants which segregated very clearly from the normal plants. This latter character has been out-crossed and again recovered, so it is a heritable change.

Abnormalities which are inherited as simple Mendelian recessives are continually being found in maize. Presumably they are due to mutation, but since they can be easily carried along in heterozygous stock there is no way of knowing when the new character actually originated. In these changes in inbred strains we have clear evidence of the occurrence of heritable variations in maize at a definite time.

Since changes in visible characters have occurred, it is possible that other variations have taken place which affect the external appearance of the plants so little that they can not be easily noted, but which at the same time make individuals from the same source germinally unlike and result in an increase in growth when the plants are crossed. On account of the likelihood of germinal changes taking place together with delayed segregation due to balanced lethals and other factorial and chromosomal complications, it is probably impossible to obtain strains which are absolutely homozygous. Before self-fertilization automatically reduces a heterozygous stock to complete uniformity and constancy, germinal changes will occur which will make some individuals heterozygous with respect to some factor pairs. From this it is evident that homozygosity

is entirely a matter of degree and that the complete state is rarely if ever attained.

INBREEDING AFTER CROSSING INBRED STRAINS

The behavior of long-inbred strains, when crossed and again inbred, demonstrates very clearly the working of hybrid vigor. After eight generations of self-fertilization two of the Leaming strains, A and B, were crossed. The first-generation hybrid was self-fertilized and each following successive inbred generation from this cross was again self-fertilized until seven inbred generations were secured. These successive inbred generations together with parental strains and their first-generation hybrid were all grown in adjoining rows each year from the time the two strains were first crossed. Single plants self-pollinated at random were used as the progenitors in each generation. The original seed was used up to the fifth generation after the cross. In that year single plants were again self-pollinated in each generation to give a fresh supply of seed. This was necessary because maize does not retain its viability and vigor long enough to complete the demonstration. The character of the progeny has depended upon the particular plant chosen as the progenitor and the results have been somewhat erratic since each generation does not have the same particular ancestor the previous generation has had. Somewhat smoother results might have been obtained by self-pollinating a large number of plants and using a composite sample of seed.

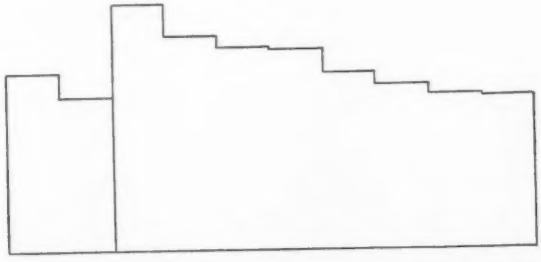
In 1923 seven successive inbred generations together with the first-generation hybrid and the two parental strains were grown in adjoining rows. Representative plants are shown in figure 2 in the order they grew in the field, making a natural curve of inbreeding. The data for average height obtained from about 50 plants in each lot are shown graphically in figure 3.

The data for length of ear for the same plants are given in figure 4. Measurements for height and length of ear are given for the one year, 1923. The production of grain was measured every year except one following the original cross, each year having one more generation than the previous. The yields obtained each year are given in table 4. The average production during six years for the parental strains, the F_1 and F_2 generations, with the later generations, each one year less, is shown graphically in figure 5. The production of grain is much more variable than the other characters measured, since yield is easily influenced by all environmental factors. The greater susceptibility of some generations to smut infection than others has been one reason for the somewhat erratic

results. The decrease in rate of growth after crossing is shown very clearly in figure 6.

The reduction in variability from the F_2 to the F_8 generation was very noticeable in the field. One of the parents has colored silks the other

FIGURE 2.—Representative plants from two long-inbred strains at the left, their first generation hybrid adjoining, followed by successive self-fertilized generations from this hybrid. Grown in adjoining rows in the same year.



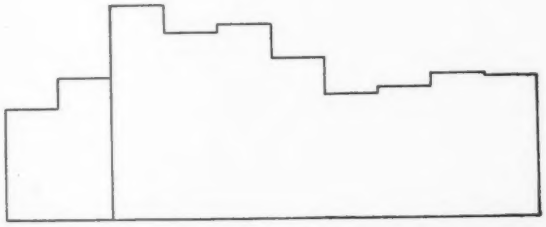
Pedigree	P'_1	P_1''	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8
Generations selfed	17	16	0	1	2	3	4	5	6	7
Height in inches	67.9	58.3	94.6	82.0	77.6	76.8	67.4	63.1	59.6	58.8

FIGURE 3.—Height of plant in successively self-fertilized generations of maize.

TABLE 4

The production of grain in bushels per acre, of two inbred strains of maize and their hybrid, from the F_1 to the F_8 generation, successively self-fertilized.

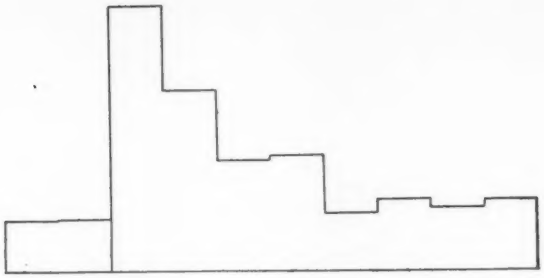
YEAR GROWN	GENERATIONS									
	P_1'	P_1''	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8
1917	5.5	21.5	64.5	56.0						
1918	23.5	26.9	120.6	128.4	15.1					
1920	27.8	16.2	127.6	47.6	34.8	29.0	9.9			
1921	13.1	19.6	72.8	54.5	49.2	32.7	15.3	23.1		
1922	26.1	20.0	160.4	83.2	73.7	67.5	48.8	35.7	22.7	
1923	21.0	13.2	61.0	45.0	40.5	47.0	15.8	23.0	26.2	27.2
Average	19.5	19.6	101.2	69.1	42.7	44.1	22.5	27.3	24.5	27.2



Pedigree	P_1'	P_1''	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8
Generations selfed	17	16	0	1	2	3	4	5	6	7
Earlength in cm.	8.4	10.7	16.2	14.1	14.7	12.1	9.4	9.9	11.0	10.7

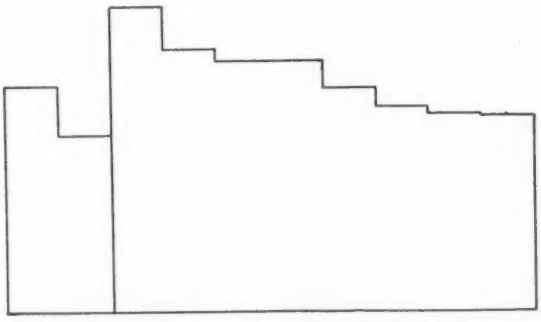
FIGURE 4.—Length of ear, in centimeters, in successively self-fertilized generations of maize.

uncolored. The F_1 plants were all colored. The F_2, F_3 and F_4 generations segregated for color, while the remaining generations were all uniformly colored. Height of plant, position of the ear on the stalk, form of tassel, and all structural details were noticeably uniform in the parents and the F_1 generation. The plants in the F_2 to F_5 generations were quite variable but later became more and more uniform, until the last two generations were as uniform as the two parental strains although differing from both in type. The behavior with respect to variability in the several



Pedigree	P_1'	P_1''	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8
Generations selfed	17	16	0	1	2	3	4	5	6	7
Yield in bushels per acre	19.5	19.6	101.2	69.1	42.7	44.1	22.5	27.3	24.5	27.2

FIGURE 5.—Yield of grain, in bushels per acre, in successively self-fertilized generations of maize.



Pedigree	P_1'	P_1''	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8
Generations selfed	17	16	0	1	2	3	4	5	6	7
Daily increase in height (inches)	.86	.67	1.16	1.00	.95	.95	.85	.78	.75	.74

FIGURE 6.—Daily increase in height in inches, in successively self-fertilized generations of maize.

generations, in height of plant, is shown graphically in figure 7.[2] The low variability of the F_4 generation is an exception to the otherwise regular reduction in variability.

[2] The two parental strains in 1923 were quite variable in height, due to some unfavorable environmental influence in the early seedling stage, which did not affect the other generations so noticeably. Since these long-inbred strains had always been exceedingly uniform previously, the data used in figure 7 for the two parental strains are from plants grown in 1922.

Pedigree	P_1'	P_1''	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_8
Generations selfed	17	16	0	1	2	3	4	5	6	7
C. V., height of plant	5.2	9.6	6.4	11.8	11.1	5.7	8.0	7.6	5.9	5.2

FIGURE 7.—Variability in height of plant in successively self-fertilized generations of maize.

DISCUSSION

This demonstration of the results of inbreeding, crossing and again inbreeding, conforms with the interpretation of hybrid vigor based upon the known facts of Mendelian heredity and chromosome behavior. Inbreeding a heterozygous stock automatically sorts out uniform and fixed types which, in the case of maize, are much reduced in size and vigor. Crossing any two of these fixed types, descended from different individuals at the start, results immediately in an increase in size and rapidity of growth. Uniformity is retained in the first generation but lost in the second. Further inbreeding again reduces size and vigor in the same way it did the first time; uniformity and fixity of type are regained at about the same rate on the average, until, in approximately the same number of generations of self-fertilization, the same level of vigor is reached. Due to recombination the resultant strains differ from their parental strains in varying degree. Since the rate at which constancy is approached may differ with the degree of heterozygosity of the progenitors chosen in each generation and their constitution with respect to specific growth factors, it is remarkable that the inbreeding process follows the same general course so closely as it does.

SUMMARY

Four strains of maize, self-fertilized eight generations or more, were each separated into two paired lines which were further self-fertilized for eight or nine generations more. The paired lines of two of these strains at the end of this period did not differ visibly in any respect. One strain differed

only in seed color while the fourth was noticeably different in many characters.

When the paired lines were crossed and the hybrids compared with their parents, there were significant increases in some characters in the strains which were visibly alike. The hybrids of the paired lines which differed in many respects were significantly increased in all characters.

After fourteen generations of self-fertilization in one strain and fifteen in another, a test for homozygosity was made by comparing the progeny from self-fertilized F_1 plants of the cross of these two diverse strains, with the progeny from intercrossed F_1 plants. No significant difference in height or production of grain was obtained.

Two germinal changes have occurred in these long-inbred strains, in such a way that they could not be due to out-crossing and were probably not due to delayed segregation.

Self-fertilizing plants produced by the crossing of two long-inbred strains, in seven successive generations, again brought about a reduction in size and rapidity of growth, and an increase in uniformity, which proceeded at approximately the same rate as when the plants were first inbred, until about the same level of vigor was established, at which time the reduction practically ceased.

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INHERITANCE OF BLACK AND RED COAT COLORS IN CATTLE*

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INTRODUCTION

BARRINGTON and PEARSON (1906) found from a study of the inheritance of blue-gray coat color in cattle that some pure-bred Galloway cows dropped red or roan calves when mated with a white Shorthorn male. LLOYD-JONES and EVVARD (1916) made a further study of inheritance of coat color in blue-gray cattle. The data for the latter study were obtained from experiments in which pure-bred and grade Galloways were mated with Shorthorns. From these matings there were obtained 78 F_1's of which 67 were black or blue-gray calves, while 11 were red or red-roan. Five of these blue-gray F_1 females were mated with a blue-gray F_1 male, producing 21 calves in the second generation. Of this number 15 showed the black pigment, while 6 showed the red. The authors explained these results by assuming that black, *B*, is dominant to red, *b*. The results obtained in the first generation were due to the fact that part of the females were homozygous for black, *BB*, while part were heterozygous, *Bb*. The F_1's mated together were *Bb* in composition and consequently were expected to produce 3 black-pigmented offspring to 1 red-pigmented. The actual result of 15 to 6 was close to this ratio. The authors conclude

* The GALTON AND MENDEL MEMORIAL FUND has met in part the cost of setting table 6.

that, "The nature of black and red pigment in cattle as an independent allelomorphic pair of characters is clearly indicated."

In discussing the roan color of the Shorthorn cattle, DUCK (1923) writes:

"The question logically arises, why will a cross between red and black produce no roans? The reason is apparent when it is considered that red and black are genetically, as well as practically, true allelomorphs, resulting in complete dominance of black in the heterozygote, which in turn will separate out in the second generation in the definite Mendelian ratio of three dominants to one recessive."

KUIPER (1921) has found from a study of the breeding of Dutch Belted cattle that some of the calves are self-colored. He states that,

"In this case they are mostly coal black, but occasionally when both parents are heterozygous as regards black hair, plain red calves were produced."

In a study of the color of the animals, as recorded in the herd-book of the AMERICAN ABERDEEN-ANGUS BREEDER'S ASSOCIATION, COLE and JONES (1920) found that the number of red animals per each thousand recorded in a volume of the herd-register ranged from 8.14 in the third volume down to .16 in the later volumes. The decrease in percentage of red animals is explained partly by the fact that red males could not be registered after volume 3, and partly because the red animals were unpopular. In addition, they believe that red is gradually being eliminated from this breed. The authors state,

"Both parents of a red calf are equally responsible for the departure from the desired color. Furthermore, from each parent there must be an unbroken line of individuals red or 'carrying red,' that is 'masqueraders,' back to the remote red animals included in the ancestry of the breed."

TEMPLETON (1923) has recently called attention to a red calf which resulted from mating a pure-bred Angus male with a pure-bred Hereford cow. He explains this by assuming that the Angus was heterozygous for coat color.

It is the purpose of this paper to present additional experimental data concerning the inheritance of black and red coat colors in cattle.

SOURCE OF MATERIAL

An experimental study of inheritance in dairy cattle was undertaken by T. J. BOWLKER of Framingham, Massachusetts, in 1911. For this purpose Mr. BOWLKER made reciprocal crosses of the Holstein-Friesian and Guernsey breeds. The work was started with 41 Holstein and 18 Guernsey females. The F_1 females resulting from the cross were kept in

the herd and were mated with F_1 males that had been selected for breeding purposes.

After the death of Mr. BOWLKER in 1917, his family undertook the completion of the work under the supervision of Doctor W. E. CASTLE. In 1919 Mrs. BOWLKER decided to discontinue the work and the herd was purchased by the UNIVERSITY OF ILLINOIS. Since that time the work has been carried on under the direction of the Department of Dairy Husbandry. A preliminary report of the experiment from 1911 to 1919 has been made by CASTLE (1919).

HYPOTHESIS

The theory that black and red in cattle are an independent allelomorphic pair of characters and that black is dominant to red will be assumed as a basis for the explanation of the results obtained in this experiment. Upon this basis the black-and-white animals are homozygous for black, *BB*, or carry the factors for both black and red, making them heterozygous, *Bb*. The red-and-white animals are homozygous for red, *bb*, regardless of the generation to which they belong. Therefore, it will not be necessary to indicate whether a red-and-white animal is pure-bred, F_1 or F_2.

PRESENTATION AND DISCUSSION OF DATA

Table 6 (appendix) shows all the matings made and animals born in the BOWLKER hybrid herd previous to November 8, 1922. It also gives the name or number, date of birth, color and sex of each animal born, together with the name, number and color of the parents. The table is so arranged that the pedigree of any individual can be traced back to the registered ancestors.

TABLE 1

Summary of the reciprocal matings of pure-bred animals showing color of offspring.

PARENTS		OFFSPRING	
Male	Female	Black-and-white	Red-and-white
Guernsey.....	Holstein	88	7
Holstein.....	Guernsey	31	0
Total.....		119	7

A summary of the matings of pure-bred animals, together with the number and color of their offspring, is given in table 1.[1] These data show that when the Holstein males were mated with the Guernsey females

[1] There have been a few animals born for which the color has not been recorded. These were mostly males, which were doubtless disposed of at birth.

all of the offspring were black and white; that when Guernsey males were mated with Holstein females the ratio was 88 black-and-white and 7 red-and-white offspring.

Fifteen calves were produced by mating Holstein females with red-and-white F_1 males, 4 by mating Guernsey females with red-and-white F_1 males, 1 by mating a Holstein female with a black-and-white F_1 male, and 1 by mating a Guernsey female with a black-and-white F_1 male. The results of these matings are shown in table 2. It will be seen from this

TABLE 2

Summary of matings of pure-bred females with F_1 males.

PARENT		OFFSPRING	
Male	Female	Black-and-white	Red-and-white
Red-and-white F_1	Holstein	14	1
Red-and-white F_1	Guernsey	0	4
Black-and-white F_1	Holstein	1	0
Black-and-white F_1	Guernsey	0	1

table that the Holstein females mated with red-and-white F_1 males produced 14 black-and-white calves to 1 red-and-white. When Guernsey females were mated with the same F_1 male, 4 red-and-white calves were produced but no black-and-white ones. The Holstein cow produced a black-and-white calf when mated with a black-and-white F_1 male, but the Guernsey cow produced a red-and-white calf when mated with the same male.

It is interesting to know that the 8 red-and-white calves produced by the Holsteins, as shown by tables 1 and 2, came from 3 cows. These three cows also produced 3 black-and-white calves. The matings of these 3 cows, together with the color of their offspring, are shown in table 3.

TABLE 3

Matings and offspring of pure-bred Holsteins which produced red-and-white calves.

RED-AND-WHITE	PURE-BRED HOLSTEIN	OFFSPRING	
Male parent	Female parent	Black-and-white	Red-and-white
Langwater Moderator 14556	Hailey Segis Erie Colantha 172915	0	1
Hailey Dimple Boy 22309	Hailey Segis Erie Colantha 172915	1	3
Hailey Dimple Boy 22309	Hailey Perfecta Clothilde 138099	1	1
Silverwood Brilliant 35980	Hailey Perfecta Clothilde 138099	0	1
Guernstein Prince F_1	Hailey Perfecta Clothilde 138099	0	1
Hailey Dimple Boy 22309	Hailey Segis Perfecta 188896	0	1
Guernstein Sultan F_1	Hailey Segis Perfecta 188896	1	0

If it is assumed that red is recessive to black, as has been previously pointed out, it would be necessary for the three Holstein cows, given in table 3, to be heterozygous for black. Accordingly, when mated with red-and-white bulls they would be expected to produce black-and-white and red-and-white calves in equal numbers. The actual result obtained was 3:8, respectively. The probable error for this result has been determined according to the method suggested by WELDON (1901). This shows the deviation to be 2.5, the probable error ± 1.1185, and deviation divided by probable error, 2.235. This shows that the result obtained is not very close to the expected numbers. However, because of the small numbers, this result should not be given much consideration.

The pedigrees of the three Holstein cows in question are presented on the following page in order that the relationship between them may be studied. Two of the cows, Hailey Segis Perfecta and Hailey Segis Erie Colantha, have the same sire, King Vernon Johanna Segis. The question arises as to whether these two cows inherited the factor for red from their sire or from their dams. Their sire, King Vernon Johanna Segis, was in the experimental herd and was used in 10 of the 31 matings with Guernsey cows which produced all black-and-white calves. Had he carried the factor for red, it would have been expected that half his calves would be black-and-white and half red-and-white, when he was mated with Guernsey cows. Instead, all ten of his calves from such matings were black-and-white. According to the theory of probabilities, this result would not have been expected more than once in 1024 times had he carried the factor for red. On this basis, it seems safe to conclude that the bull was homozygous for black, and therefore could not have transmitted the factor for red to his daughters.

Since the two cows, Hailey Segis Perfecta and Hailey Segis Erie Colantha, did not inherit the factor for red from their sire they must have inherited it through their dams. This is quite evident in the case of the former, since it is known that her dam, Hailey Perfecta Clothilde, carried the factor for red because she produced three red-and-white calves out of four matings to red-and-white males. There is no direct evidence that Hailey Erie Colantha, the dam of Hailey Segis Erie Colantha, carried the factor for red; but from the data presented it seems safe to conclude that she was heterozygous.

It is impossible to determine which animals, in the pedigrees of Hailey Erie Colantha and Hailey Perfecta Clothilde, carried the factor for red. All of the registered animals in their pedigrees were black-and-white and did not produce, so far as is known, any red-and-white offspring. The

- **Hailey Perfecta Clothilde 138689**
  - Sir Netherland Clothilde Colantha 27989
    - Sir Netherland Clothilde 8517
      - Clothilde 4th's Imperial 1281
      - Netherland Princess 5th 1598
    - De Vries Netherland Clothilde 41537
      - Soldene 2nd's Netherland 8519
      - De Vries 3rd's Colantha 27059
  - Walnut Hills Perfecta 81598
    - Johanna DeKol's Sarcastic Lad 28303
      - Sarcastic Lad 23971
      - Johanna DeKol 36478
    - Goddard Pet 57371
      - Concordia 2nd's Paul DeKol 21430
      - Montague Maid 50940
- **Hailey Segis Erie Colantha 172915**
  - King Vernon Johanna Segis 59332
    - King Segis 36168
      - Mercedes Julip's Pietertje Paul 29830
      - A. & G. Inka McKinley 55163
    - Johanna Vernon DeKol 70943
      - Johanna Rue 3rd's Lad 26939
      - Susie Vernon DeKol 53671
  - Hailey Erie Colantha 112226
    - Prince Dexter Johanna 43819
      - Colantha Johanna Lad 32481
      - Princess Dexter 53010
    - Hazel Erie 68719
      - Duke of Erie 28030
      - Hazel Ophelia Queen 55078
- **Hailey Segis Perfecta 188896**
  - King Vernon Johanna Segis 59332
    - King Segis 36168
      - Mercedes Julip's Pietertje Paul 29830
      - A. & G. Inka McKinley 55163
    - Johanna Vernon DeKol 70943
      - Johanna 3rd's Lad 26939
      - Susie Vernon DeKol 53671
  - Hailey Perfecta Clothilde 138689
    - Sir Netherland Clothilde Colantha 27989
      - Sir Netherland Clothilde 8517
      - De Vries Netherland Colantha 41537
    - Walnut Hills Perfecta 81598
      - Johanna DeKol's Sarcastic Lad 28303
      - Goddard Pet 57371

factor for red can be accounted for only on the basis that it was carried by one animal in each generation of each pedigree back to the time when red-and-white animals appeared among the ancestors. This shows that the factor for red may be carried through many generations without the appearance of red hair. Likewise, this factor is doubtless carried by an unknown number of pure-bred Holsteins at the present time.

TABLE 4

Number and color of animals obtained from F_1 matings

COLOR OF PARENTS		OFFSPRING		DEVIATION	PROBABLE ERROR	DEV. / P. E.
Male	Female	Black-and-white	Red-and-white			
Red-and-white.....	Black-and-white...	33	31	1.00	±2.698	.371
Red-and-white.....	Red-and-white....	0	3			
Black-and-white....	Black-and-white...	21	8	.75	±1.573	.476
Black-and-white....	Red-and-white....	0	0			

A summary of the F_1 matings is given in table 4. This shows that when the red-and-white F_1 males were mated with the black-and-white F_1 females there were produced 64 offspring, of which 33 were black-and-white, and 31 were red-and-white. There were only 3 matings in which these same males were mated with red-and-white females, but all the offspring were red-and-white. When the black-and-white F_1 male was mated with females of the same color the result was 21 black-and-white to 8 red-and-white offspring. There were no matings of the black-and-white male with red-and-white females.

In accordance with the postulated theory, the black-and-white F_1 animals may be considered to be heterozygous for color, whereas the red-and-white animals may be considered to be homozygous for red. Consequently, when matings were made between the black-and-white and red-and-white an equal number of each color would be expected in the offspring. The result of 33 to 31 agrees very well with the expected numbers, as shown by the probable error in table 4.

The black-and-white F_1's, when mated together, would be expected to produce black-and-white and red-and-white offspring in the ratio of 3 to 1, respectively. As shown by table 4 the result 21 to 8, respectively, is very close to the expected ratio. Since the red-and-white animals are homozygous for the recessive red factor, they would produce only red-and-white offspring when mated together. This was the result obtained with three matings.

Only a few F_2 females in the herd have freshened up to the present time. Some of these were mated with F_1 males and some with pure-breds. A

few three-quarter-blood females[2] also have been mated with F_1 or pure-bred males. A summary of these matings, which are given in table 6 (appendix), is given in table 5. Since the animals represented by this table are not all of the same generation, the genetic composition of each group is indicated. The black-and-white three-quarter-bloods, F_1's and F_2's, with the possible exception of 724 (see note 3, table 6, appendix) are

TABLE 5

Summary of matings of F_2 and three-quarter-blood females with F_1 and pure-bred males.

MALE PARENTS		FEMALE PARENTS		OFFSPRING	
Color	Genetic composition	Color	Genetic composition	Black-and-white	Red-and-white
Red-and-white	*b b*	Red-and-white	*b b*	0	6
Red-and-white	*b b*	Black-and-white*	*B b*	3	2
Black-and-white F_1	*B b*	Red-and-white	*b b*	5	3
Black-and-white F_1	*B b*	Black-and-white	*B b*	6	2
Black-and-white (Registered Holstein)	*B B*	Red-and-white	*b b*	5	0
Black-and-white (Registered Holstein)	*B B*	Black-and-white	*B b*	4	0

* It is possible that one of these F_2 females, 724, is homozygous, *BB*.

heterozygous, *Bb*. Although mated with red-and-white and heterozygous black-and-white females the two registered Holstein males have never sired a red-and-white calf, so they are considered homozygous, *BB*. The numbers obtained from these matings are small, but may well be considered.

When the red-and-white animals were mated together they produced only red-and-white offspring, as would be expected. The next two types of matings in the table may be considered together, for one parent is red-and-white, while the other is heterozygous. The results of these two types of matings are 8 black-and-white to 5 red-and-white, while an equality would be expected. As stated above, one of these F_2 parents considered to be heterozygous may be homozygous for black. This may account for one of the black-and-white offspring which should not be included in the ratio. The mating together of black-and-white F_1's, or heterozygous animals, gave a result of 6:2, respectively, which is a ratio of 3 to 1, as would be expected. The pure-bred Holsteins produced only black-and-white offspring when mated to both red-and-white and heterozygous black-and-white animals. This is to be expected with pure-bred Holsteins that are homozygous for black.

[2] The animals which have one F_1 parent and the other a pure-bred are referred to as three-quarter-bloods.

The results obtained from this experiment bear out the theory that black is dominant to red and that the two pigments act as an independent allelomorphic pair of characters.

There is some variation in the intensity of black and red colors of the animals in the BOWLKER hybrid herd. Some are a jet black with white, while others are a brownish black or chocolate and white. The original records kept by Mr. BOWLKER report some of these animals as "seal color and white." The red color varies from a very dark to a light red. The intensity of the black may be explained on the same basis as LLOYD-JONES and EVVARD (1916) explain the variation in the black of the Galloways. In regard to this condition they state,

> "This is produced by weakening or failure of the black in the tips of the hairs and its replacement by a rusty red pigment. . . . The rusty appearance so often observed in Galloways is not a criterion as to the purity of these animals for the black factor and is in fact quite unrelated genetically to the condition known as red."

It is hoped that a further study of this color may be made on the animals in the BOWLKER hybrid herd.

SUMMARY AND CONCLUSIONS

In 1911 T. J. BOWLKER started reciprocal crosses between Holsteins and Guernseys in order to study the inherited characteristics of dairy cattle. The experiment was later taken over by the UNIVERSITY OF ILLINOIS. The data obtained by this experiment furnish material for the study of the inheritance of black and red coat colors in cattle.

The matings which have been made in the experimental herd number 291.

Three Holstein cows dropped red-and-white calves when mated with red-and-white males. This is evidence that some pure-bred Holstein cattle carry the factor for red.

The data presented conform to the proposition that black and red coat colors in cattle are an allelomorphic pair of characters, and that black is dominant to red.

The intensity of the color of the pigmented areas varies from a jet black to a brownish black or chocolate in the case of the black-and-white animals, and from a dark to a light red in the red-and-white animals.

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APPENDIX

In order to save space in the following table the male is referred to by the initials. The names and numbers (when registered) which correspond to the initials given in the table are as follows:

Initial		*Name*	*Number*	*Breed*
L. M.	=	Langwater Moderator	14556	Guernsey
H. D. B.	=	Hailey Dimple Boy	22309	Guernsey
S. B.	=	Silverwood Brilliant	35980	Guernsey
A. V. F. P.	=	Archer's Victor of Four Pine	67661	Guernsey
I. V. K.	=	Illini Victoria King	68560	Guernsey
I. M. K. Y.	=	Illini May King Yeksa	59565	Guernsey
K. V. J. S.	=	King Vernon Johanna Segis	59332	Holstein
H. S. E.	=	Hailey Segis Elliston	170069	Holstein
O. C. H.	=	Ona Clothilde Hartog	226637	Holstein
I. J. O.	=	Illini Johanna Ona	349919	Holstein
G. P.	=	Guernstein Prince	.....	F_1
G. S.	=	Guernstein Sultan	.....	F_1
G. D.	=	Guernstein Duke	.....	F_1
No. 3	=	a No. 3	.....	F_1

TABLE 6

Breeding, date of birth, color and sex of animals born in Bowker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number*	Color					
L. M.	R & W	Hailey Segis Erie Colantha	172915	B & W	a Sultan	—	9–20–12	R & W	♂
L. M.	R & W	Halley Katy DeKol	136550	B & W	a Robert	—	12– 2–12	B & W	♂
K. V. J. S.	B & W	College Girl of Haddon	23870	R & W	a William	—	2–28–13	B & W	♂
K. V. J. S.	B & W	Rockbottom Keepsake	34511	R & W	a Henry	—	3– 8–13	B & W	♂
K. V. J. S.	B & W	Lady of Maple Farm	25375	R & W	a Joseph	—	3–29–13	B & W	♂
K. V. J. S.	B & W	Glenstay's Foam	25657	R & W	a Mary	—	3–29–13	B & W	♀
K. V. J. S.	B & W	Gloria of Chatham	17058	R & W	a Kate	652	4–24–13	B & W	♀
L. M.	R & W	Hailey Segis Wachusett	171116	B & W	a Delia	—	5– 4–13	B & W	♀
H. D. B.	R & W	Hailey Segis Twisk	171115	B & W	a Ellen	651	10– 4–13	B & W	♀
H. D. B.	R & W	Hailey Veldoor Clothilde DeKol	99377	B & W	a Blackfoot	653	10–19–13	B & W	♀
H. D. B.	R & W	Hailey Julipana DeKol	99376	B & W	a Sealskin	—	10–31–13	B & W	♀
H. D. B.	R & W	H. Landor Whitstone DeKol	221081	B & W	a Jane	654	11–30–13	B & W	♀
H. D. B.	R & W	Judy Clothilde DeKol	62217	B & W	a Julia	—	12– 6–13	B & W	♀
H. D. B.	R & W	Halley Belle Twisk	136892	R & W	a Fannie	655	12–14–13	B & W	♀
K. V. J. S.	B & W	Rockbottom Leading Lady	34510	R & W	a Daisy	661	12–24–13	B & W	♀
K. V. J. S.	B & W	Hailey Maid	32515	R & W	a Richard	—	12–26–13	B & W	♂
H. D. B.	R & W	H. Alice Creamelle DeKol	135585	B & W	a Dora	656	1– 2–14	B & W	♀
H. D. B.	R & W	Hailey Montello Creamelle DeKol	135589	B & W	a Stephen	—	1– 3–14	B & W	♂
H. D. B.	R & W	Hailey Pauline Colantha DeKol	135587	B & W	a Charlie	—	1– 5–14	B & W	♂
H. D. B.	R & W	Hailey Burke Inka DeKol	112077	B & W	a Emma	666	1– 9–14	B & W	♀
H. D. B.	R & W	Hailey Judy Creamelle DeKol	135583	B & W	a Annie	670	1–10–14	B & W	♀
K. V. J. S.	B & W	Halley Katy Belle	32704	R & W	a Belle	—	1–23–14	B & W	♀
H. D. B.	R & W	Halley Katy DeKol	136550	B & W	a Rosie	—	1–26–14	B & W	♀
H. D. B.	R & W	Halley Tessa Netherland	136551	B & W	a Tessa	—	1–28–14	B & W	♀

*The larger numbers are the registration numbers of pure-bred animals, while the three-place numbers are the herd numbers given at the UNIVERSITY OF ILLINOIS.

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
H. D. B.	R & W	Hailey Hazel Pietertje Colantha.	221084	B & W	a George	—	2- 1-14	B & W	♂
K. V. J. S.	B & W	Rockbottom Keepsake	34511	R & W	a Polly	—	2- 6-14	B & W	♀
H. D. B.	R & W	Hailey Inka Colantha DeKol	135588	B & W	a Canute	—	2- 7-14	B & W	♂
H. D. B.	R & W	Hailey Segis Perfecta	188896	B & W	a Guernstein Prince	—	2-18-14	R & W	♂
H. D. B.	R & W	Hailey Segis Erie Colantha	172915	B & W	a Harold	—	2-21-14	B & W	♂
H. D. B.	R & W	H. Pauline Dot DeKol	112078	B & W	a Paulina	—	2-22-14	B & W	♀
K. V. J. S.	B & W	Glenstay's Foam	25657	R & W	a Foam	—	3-11-14	B & W	♀
H. D. B.	R & W	Hailey Segis Wachusett	171116	B & W	a Agnes	—	5- 1-14	B & W	♀
H. D. B.	R & W	DeKol Paul Elliston	87450	B & W	a 14	—	7-30-14	B & W	♂
H. D. B.	R & W	Hailey Segis Judy Colantha Univ. of Ill. Herd No	190082 632	B & W	a 16	—	8-15-14	B & W	♂
H. S. E.	B & W	Hailey Dimple Keepsake	40786	R & W	a Aster	—	8-28-14	B & W	♀
H. S. E.	B & W	Hailey Dimple Modena	40787	R & W	a Dimple	—	9- 9-14	B & W	♀
H. D. B.	R & W	Hailey Segis Inka Univ. of Ill. Herd No	188894 633	B & W	a Inka	—	9-21-14	B & W	♀
H. D. B.	R & W	Hailey Segis Katherine Univ. of Ill. Herd No	188895 634	B & W	a Peach	—	9-27-14	B & W	♀
H. D. B.	R & W	Montello Pieterje	72061	B & W	a 18	—	10- 3-14	B & W	♂
H. D. B.	R & W	Hailey Segis Twisk	171115	B & W	a Twisk	657	10- 4-14	B & W	♀
H. D. B.	R & W	H. Segis Dot Elliston	189444	B & W	a 17	—	10- 8-14	B & W	♂
H. S. E.	B & W	Hailey All Fawn	40785	R & W	a Grace	—	10-10-14	B & W	♀
H. D. B.	R & W	H. Veldoor Clothilde DeKol	99377	B & W	a Lilac	—	10-17-14	B & W	♀
H. D. B.	R & W	Hailey Segis Veldoor	188897	B & W	a Peggy	—	10-23-14	B & W	♀
H. D. B.	R & W	Hailey Colantha Plum	215637	B & W	a Pearl	658	11- 4-14	B & W	♀
H. S. E.	B & W	Hailey Haddon Dairymaid	40858	R & W	a Nancy	660	11- 5-14	B & W	♀
H. S. E.	B & W	Queen of Maplehurst	19438	R & W	a Freckles	659	11- 8-14	B & W	♀
H. D. B.	R & W	Judy Clothilde DeKol	62217	B & W	a 19	—	12- 7-14	B & W	♂

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
H. D. B.	R & W	Drynock Esther	84479	B & W	a Esther	—	12–19–14	B & W	♀
H. D. B.	R & W	H. Melaine Judy Colantha	135582	B & W	a Sylvene	665	1– 1–15	B & W	♀
H. D. B.	R & W	H. Creamelle Mercedes DeKol	112074	B & W	a 20	—	1– 5–15	B & W	♂
H. D. B.	R & W	Hailey Segis Judy	171119	B & W	a 21	—	1–12–15	B & W	♂
H. S. E.	B & W	Hailey Maid	32515	R & W	a Ruby	—	1–15–15	R & W	♀
H. D. B.	R & W	H. Segis Erie Vernon	190081	B & W	a Bessie	—	1–18–15	B & W	♀
H. D. B.	R & W	H. Burke Inka DeKol	112077	B & W	a 22	—	1–19–15	B & W	♂
H. S. E.	B & W	Hailey Gloria	40784						
		Univ. of Ill. Herd No	636	R & W	a 23	—	1–21–15	B & W	♂
H. S. E.	B & W	Hailey Katy Belle	32704	R & W	———	—	1–26–15	B & W	♂
H. D. B.	R & W	H. Inka Colantha DeKol	135588	B & W	a Fanniel	662	2– 3–15	B & W	♀
H. S. E.	B & W	Lady of Maple Farm	25375	R & W	a Lilvene	—	2–10–15	B & W	♀
H. D. B.	R & W	H. Montello Creamelle DeKol	135589	B & W	a Lavaine	—	2–10–15	B & W	♀
H. D. B.	R & W	Hailey Julipana DeKol	99376	B & W	a Alice	—	2–26–15	B & W	♀
G. S.	R & W	H. Segis Dexter Erie	220674	B & W	———	—	3– 2–15	B & W	♂
H. D. B.	R & W	H. Alice Creamelle DeKol	135585	B & W	a 25	—	3–17–15	B & W	♂
H. D. B.	R & W	Halley Katy DeKol	136550	B & W	a 26	—	3–26–15	B & W	♂
H. S. E.	B & W	Glenstay's Foam	25657	R & W	a 27	—	4– 8–15	B & W	♂
H. D. B.	R & W	H. Segis Erie Colantha	172915	B & W	a Guernstein Queen	—	4–14–15	R & W	♀
H. D. B.	R & W	H. Pauline Colantha DeKol	135587	B & W	a 28	—	4–18–15	B & W	♂
H. D. B.	R & W	H. Judy Creamelle DeKol	135583	B & W	a Emerald	663	5– 8–15	B & W	♀
H. D. B.	R & W	Hailey Segis Alice	220675	B & W	a Sapphire	—	5–22–15	B & W	♀
H. D. B.	R & W	Hailey Montello Segis	220673	B & W	a 29	—	6– 8–15	B & W	♂
H. D. B.	R & W	Hailey Segis Julipana	190083	B & W	a Susan	—	8–21–15	B & W	♀
G. S.	R & W	Hailey Dimple Lady	41127	R & W	Guernlady	667	8–29–15	R & W	♀
G. S.	R & W	Hailey Segis Perfecta	188896	B & W	Holfecta	668	8–30–15	B & W	♀
H. D. B.	R & W	Hailey Perfecta Clothilde	138089	B & W	a Guernstein Duke	—	9– 1–15	R & W	♂
		Univ. of Ill. Herd No	631						

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
H. D. B.	R & W	Hailey Segis Wachusett	171116	B & W	α Wachusa	—	9- 6-15	B & W	♀
G. P.	R & W	Hailey Modena Maid	48037	R & W	Guerndena	669	9-26-15	R & W	♀
G. P.	R & W	H. Segis Vernon Julipana	189445	B & W	Holvern	—	10- 6-15	B & W	♂
G. P.	R & W	Hailey Segis Landor	221082	B & W	Hol-Landora	—	10-23-15	B & W	♀
H. D. B.	R & W	Hailey Segis Veldoor	188897	B & W	α 33	—	11- 1-15	B & W	♂
H. S. E.	B & W	Queen of Maplehurst	19438	R & W	α 35	—	11-10-15	B & W	♂
H. S. E.	B & W	Hailey Contour Dimple	48039	R & W	α 36	—	11-11-15	B & W	♂
H. D. B.	R & W	H. Segis Judy Colantha Univ. of Ill. Herd No	190082 632	B & W	α 36	—	12-14-15	B & W	♂
G. S.	R & W	DeKol Paul Elliston	87450	B & W	Hol-Elliston	671	12-21-15	B & W	♀
H. D. B.	R & W	H. Landor Whitstone DeKol	221081	B & W	α 37	—	1- 6-16	B & W	♂
G. S.	R & W	α Kate	652	B & W	β 2	—	1- 9-16	B & W	♂
H. D. B.	R & W	Hailey Burke Inka DeKol	112077	B & W	α 40	—	1-12-16	B & W	♂
H. D. B.	R & W	Hailey Hazel Pietertje Colantha	221084	B & W	α Blossom	672	1-15-16	B & W	♀
H. S. E.	B & W	Hailey Maid	32515	R & W	α Maid	682	1-20-16	B & W	♀
G. P.	R & W	α Blackfoot	653	B & W	β 3	—	1-25-16	B & W	♂
H. S. E.	B & W	Hailey All Fawn	40785	R & W	α 42	—	1-24-16	B & W	♂
H. D. B.	R & W	Hailey Creamelle Mercedes DeKol	112074	B & W	α Sunny	—	2- 1-16	B & W	♀
H. D. B.	R & W	Judy Clothilde DeKol	62217	B & W	α 44	—	2- 1-16	B & W	♂
H. S. E.	B & W	Judy Haddon Dairymaid	40858	R & W	α 45	—	2- 1-16	B & W	♂
H. D. B.	R & W	Hailey Segis Inka Univ. of Ill. Herd No	188894 633	B & W	α Sally	677	2- 2-16	B & W	♀
H. D. B.	R & W	Hailey Segis Twisk	171115	B & W	α Seville	673	2- 8-16	B & W	♀
G. S.	R & W	H. Alice Creamelle DeKol	135585	B & W	Hol-Alice	—	2-13-16	B & W	♀

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
H. S. E.	B & W	Lady of Maple Farm	25375	R & W	α Lady	—	2–21–16	B & W	♀
H. D. B.	R & W	Hailey Segis Judy	171119	B & W	α Judy	—	2–25–16	B & W	♀
H. D. B.	R & W	Hailey Montello Creamelle DeKol	135589	B & W	α 46	—	2–26–16	B & W	♂
H. D. B.	R & W	Hailey Melaine Judy Colantha	135582	B & W	α Melaine	—	3– 6–16	B & W	♀
H. D. B.	R & W	Hailey Segis Erie Vernon	190081	B & W	α Erie	685	3–14–16	B & W	♀
H. S. E.	B & W	Hailey Katy Belle	32704	R & W	α Katie Belle	—	3–15–16	B & W	♀
G. S.	R & W	α Rosie		B & W	β Rosie	—	3–22–16	—	♀
H. D. B.	R & W	Hailey Pauline Colantha DeKol	135587	B & W	α 48	—	4– 8–16	B & W	♂
H. D. B.	R & W	Hailey Segis Erie Colantha	172915	B & W	α Colerie	674	4–11–16	R & W	♀
H. D. B.	R & W	Hailey Julipana DeKol	99376	B & W	α 49	—	4–17–16	B & W	♂
G. S.	R & W	Hailey Katy DeKol	136550	B & W		—	4–26–16	B & W	♂
H. S. E.	B & W	Hailey Gloria Univ. of Ill. Herd No	40784 636	R & W	α 51	—	4–29–16	B & W	♂
G. S.	R & W	Hailey Dimple Modena	40787	R & W	Modena	686	5– 5–16	R & W	♀
H. D. B.	R & W	Hailey Veldoor Clothilde DeKol	99377	B & W	α Verna	675	5–16–16	B & W	♀
H. D. B.	R & W	Hailey Segis Katherine Univ. of Ill. Herd No	188895 634	B & W	α Katha	680	5–17–16	B & W	♀
H. D. B.	R & W	Hailey Judy Creamelle DeKol	135583	B & W	α 52	—	5–20–16	B & W	♂
H. D. B.	R & W	Hailey Montello Segis	220673	B & W	α 53	—	5–29–16	B & W	♂
H. D. B.	R & W	Hailey Segis Clothilde	220672	B & W	α Twinny	—	6– 3–16	B & W	♀
H. D. B.	R & W	Hailey Segis Clothilde Univ. of Ill. Herd No	220672 635	B & W	α Twin	—	6– 3–16	B & W	♀
G. P.	R & W	α Tessa	———	B & W	β 4	—	7–17–16	B & W	♂

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
H. D. B.	R & W	Hailey Perfecta Clothilde Univ. of Ill. Herd No.	138087 631	B & W	α Perfecta	—	8- 2-16	B & W	♀
G. P.	R & W	α Daisy	661	B & W	β 5	—	8- 6-16	B & W	♂
G. P.	R & W	α Fannie	655	B & W	β 6	—	8-11-16	B & W	♂
H. D. B.	R & W	Hailey Segis Wachusett	171116	B & W	α Wacha	676	8-18-16	B & W	♀
H. S. E.	B & W	Hailey Modena Maid	48037	R & W	α Modmaida	678	9-14-16	B & W	♀
G. P.	R & W	α Julia	———	B & W	β Guernstein Emperor 7	—	10- 1-16	R & W	♂
G. P.	R & W	α Dora	656	B & W	β Dora	707	10- 6-16	B & W	♀
H. D. B.	R & W	Hailey Segis Landor	221082	B & W	α Lucy	—	11- 3-16	B & W	♀
G. S.	R & W	α Ellen	651	B & W	β Ellen	706	11-30-16	B & W	♀
G. P.	R & W	α Lilac	———	B & W	β 8	—	12- 8-16	R & W	♂
G. P.	R & W	α Mary	———	B & W	β Guernstein Leader No. 1	—	12-26-16	R & W	♂
H. D. B.	R & W	Hailey Segis Vernon Julipana	189445	B & W	α 72	—	1- 1-17	B & W	♀
G. P.	R & W	α Freckles	659	B & W	β 9	—	1- 1-17	R & W	♂
H. D. B.	R & W	Hailey Segis Judy Colantha Univ. of Ill. Herd No.	190082 632	B & W	———	—	1- 8-17	B & W	♂
H. D. B.	R & W	Hailey Landor Whitstone DeKol	221081	B & W	———	—	1- 9-17	———	♂
H. D. B.	R & W	Hailey Creamelle Mercedes DeKol	112074	B & W	———	—	1-11-17	———	♂
G. S.	R & W	α Jane	654	B & W	β 10	—	1-19-17	R & W	♂
S. B.	R & W	Hailey Segis Twisk	171115	B & W	α Martha	688	1-29-17	B & W	♀
G. P.	R & W	α Peach	———	B & W	β Jewel	703	2- 1-17	R & W	♀
G. P.	R & W	α Inka	———	B & W	———	—	2- 2-17	———	♀
G. P.	R & W	α Sylvene	665	B & W	———	—	2-22-17	R & W	♂

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
G. P.	R & W	α Peggy	———	B & W	———	—	2–28–17	B & W	♂
S. B.	R & W	DeKol Paul Elliston	87450	B & W	———	—	3– 4–17	———	♂
G. P.	R & W	α Faniel	662	B & W	β Rosy	705	3–14–17	R & W	♀
H. D. B.	R & W	Hailey Segis Pietertje Univ. of Ill. Herd No	302034 630	B & W	α Star	681	3–15–17	B & W	♀
G. P.	R & W	α Twisk	657	B & W	———	—	3–19–17	———	♀
G. P.	R & W	α Pearl	658	B & W	———	—	3–30–17	———	♂
H. D. B.	R & W	Hailey Segis Erie Colantha	172915	B & W	———	—	5– 3–17	R & W	♂
H. D. B.	R & W	Hailey Montello Creamelle DeKol	135589	B & W	α Theresia	687	5– 5–17	B & W	♀
H. D. B.	R & W	Hailey Katy DeKol	136550	B & W	α Dorothy	—	5– 7–17	B & W	♀
S. B.	R & W	Hailey Segis Whitstone	302033	B & W	———	—	5– 7–17	B & W	♂
G. P.	R & W	α Nancy	660	B & W	———	—	5–12–17	R & W	♂
H. D. B.	R & W	Hailey Segis Clothilde Univ. of Ill. Herd No	220672 635	B & W	———	—	6–10–17	B & W	♂
S. B.	R & W	Hailey Segis Katherine Univ. of Ill. Herd No	188895 634	B & W	———	—	6–17–17	B & W	♂
H. D. B.	R & W	Hailey Julipana DeKol	99376	B & W	α Kathleen	684	6–27–17	B & W	♀
S. B.	R & W	Hailey Perfecta Clothilde Univ. of Ill. Herd No	138689 631	B & W	———	—	7–22–17	R & W	♂
G. P.	R & W	α Tessa	———	B & W	β Dorise	702	7–23–17	R & W	♀
H. D. B.	R & W	Hailey Melaine Judy Colantha	135582	B & W	α Elizabeth	689	7–29–17	B & W	♀
G. P.	R & W	Guernstein Queen	———	R & W	β 1	708	8– 4–17	R & W	♀
G. P.	R & W	α Emma	666	B & W	β 2	701	8–23–17	B & W	♀

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
S. B.	R & W	Hailey Veldoor Clothilde DeKol.	99377	B & W	α 3	—	8-25-17	B & W	♂
H. D. B.	R & W	Hailey Montello Segis	220673	B & W	α 5	683	9-12-17	B & W	♀
G. P.	R & W	α Fannie	655	B & W	β 4	—	9-16-17	R & W	♂
G. P.	R & W	α Susan	———	B & W	β 6	—	9-19-17	B & W	♀
G. D.	R & W	α Grace	———	B & W	β 9	704	9-26-17	B & W	♀
G. P.	R & W	α Daisy	661	B & W	β 7	—	9-27-17	R & W	♂
G. P.	R & W	α Mary	———	B & W	β 8	—	9-28-17	B & W	♂
G. P.	R & W	α Lilac	———	B & W	β 10	—	11-15-17	———	♂
G. P.	R & W	α Ellen	651	B & W	β 11	712	11-18-17	B & W	♀
G. P.	R & W	α Blackfoot	653	B & W	β 13	—	12-11-17	R & W	♂
S. B.	R & W	Hailey Segis Twisk	171115	B & W	α 14	—	12-12-17	B & W	♂
G. P.	R & W	α Julia	———	B & W	β 15	—	12-17-17	B & W	♂
G. P.	R & W	α Dora	656	B & W	β 17	—	1-18-18	R & W	♀
G. P.	R & W	α Freckles	659	B & W	β 18	711	2-16-18	B & W	♀
G. D.	R & W	Guernlady	667	R & W	———	650	3- 1-18	R & W	♀
G. P.	R & W	α Jane	654	B & W	β 21	709	3-27-18	R & W	♀
G. P.	R & W	α Bessie	———	B & W	β 24	714	4- 4-18	R & W	♀
G. P.	R & W	Hol-Elliston	671	B & W	———	—	4- 6-18	R & W	♂
H. S. E.	B & W	Lady of Maple Farm	25375	R & W	α 23	—	4-17-18	B & W	♂
G. D.	R & W	Hailey Segis Katherine Univ. of Ill. Herd No	188895 634	B & W	27	—	6- 6-18	B & W	♂
G. P.	R & W	α Ruby	———	B & W	β 28	—	7-17-18	B & W	♂
G. P.	R & W	α Sylvene	665	B & W	β 29	—	8- 8-18	———	♀
G. P.	R & W	α Twisk	657	B & W	β 30	—	8-10-18	B & W	♀
G. P.	R & W	α Guerndena	669	R & W	———	—	9-24-18	R & W	♂
G. P.	R & W	Hailey Perfecta Clothilde Univ. of Ill. Herd No	138689 631	B & W	———	—	10- 2-18	R & W	♀

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
G. D.	R & W	α Melaine	———	B & W	β 33	—	10–29–18	B & W	♂♀
G. P.	R & W	α Mary	———	B & W	β 34	710	11– 5–18	R & W	♀
G. D.	R & W	α Katy Belle	———	B & W	β 35	—	11– 7–18	R & W	♂♀
G. D.	R & W	α Colerie	674	R & W	β 36	—	11–18–18	R & W	♀
G. P.	R & W	α Pearl	658	B & W	β 37	—	11–23–18	R & W	♂♀
G. P.	R & W	α Alice	———	B & W	β 38	713	12– 7–18	B & W	♀
G. D.	R & W	Holfecta	668	B & W	———	—	12–19–18	R & W	♂♀
G. P.	R & W	α Daisy	661	B & W	β 39	715	1–26–19	R & W	♀
G. D.	R & W	α Twin	———	B & W	β 42	723	1–31–19	B & W	♀
G. P.	R & W	α Annie	670	B & W	β 43	—	2– 3–19	R & W	♂♀
G. D.	R & W	α Perfecta	———	B & W	β 50	717	2– 9–19	B & W	♀
No. 3	B & W	α No. 5	683	B & W	β 45	—	2–21–19	B & W	♂♂
G. P.	R & W	α Emerald	663	B & W	β 46	—	3– 6–19	B & W	♂
G. P.	R & W	Hailey Segis Judy Colantha Univ. of Ill. Herd No	190082 632	B & W	———	—	3–11–19	B & W	♂
G. P.	R & W	α Ellen	651	B & W	β 48	—	3–21–19	B & W	♂
G. P.	R & W	α Blackfoot	653	B & W	β 49	—	3–28–19	B & W	♂♂
G. P.	R & W	α Jane	654	B & W	β 50	—	3–31–19	R & W	♂
G. P.	R & W	Hailey Gloria Univ. of Ill. Herd No	40784 636	R & W	———	—	4– 6–19	R & W	♂
G. P.	R & W	α Nancy	660	B & W	β 52	—	4–11–19	R & W	♀
G. P.	R & W	Hailey Segis Clothilde Univ. of Ill. Herd No	220672 635	B & W	635d3	—	4–14–19	B & W	♀
G. P.	R & W	α Faniel	662	B & W	β 54	719	4–18–19	B & W	♀
G. P.	R & W	α Verna	675	B & W	β 55	720	5– 2–19	R & W	♀

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
G. P.	R & W	Hailey Segis Inka	188894						
		Univ. of Ill. Herd No	633	B & W	633d3	—	5- 7-19	B & W	♀
G. P.	R & W	α Fannie	655	B & W	β 57	718	5-14-19	R & W	♀
G. P.	R & W	Hailey Segis Katherine	188895						
		Univ. of Ill. Herd No	634	B & W	634d	721	6-29-19	B & W	♀
G. P.	R & W	α Saphire	—	B & W	β 61	716	7-17-19	B & W	♀
No. 3	B & W	α Modmaida	678	B & W	β 678d1	—	9- 6-19	R & W	♀
No. 3	B & W	Hailey Perfecta Clothilde	138689						
		Univ. of Ill. Herd No	631	B & W	631d3	—	9-12-19	B & W	♀
G. P.	R & W	α Blossom	672	B & W	β 672s1	—	9-15-19	B & W	♂
G. P.	R & W	α Freckles	659	B & W	β 659s2	—	9-18-19	B & W	♂
No. 3	B & W	β Rosy	705	R & W	705d1	—	9-19-19	B & W	♀
G. P.	R & W	Guerndena	669	R & W	669s2	—	9-28-19	R & W	♂
No. 3	B & W	α Star	681	B & W	β 681s1	—	10- 6-19	R & W	♂
No. 3	B & W	β 2	701	B & W	701d1	—	10-17-19	B & W	♀
No. 3	B & W	α Maid	682	B & W	β 682d1	—	10-18-19	B & W	♀
No. 3	B & W	α Sally	677	B & W	β 677s1	—	10-19-19	B & W	♂
No. 3	B & W	Hailey Gloria Dimple							
		Univ. of Ill. Herd No	637	R & W	637d1	649	10-22-19	R & W	♀
No. 3	B & W	β Ellen	706	B & W	706d1	—	10-30-19	B & W	♀
No. 3	B & W	α Erie	685	B & W	β 685s1	—	11- 2-19	B & W	♂
No. 3	B & W	β Jewel	703	R & W	703d1	—	11- 7-19	B & W	♀
No. 3	B & W	β 9	704	B & W	704d1	—	11-16-19	R & W	♀
G. P.	R & W	α Sylvene	665	B & W	β 656d2	—	11-18-19	B & W	♀

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
No. 3	B & W	Holfecta	668	B & W	668d1	—	12–17–19	R & W	♀
G. P.	R & W	α Nancy	660	B & W	β 660d2	—	1– 4–20	R & W	♀
G. P.	R & W	α Pearl	658	B & W	β 658s3	—	1–10–20	R & W	♂
No. 3	B & W	α Modena	686	R & W	686s1	—	1–17–20	R & W	♂
No. 3	B & W	α No. 5	683	B & W	β 683d1	—	1–22–20	B & W	♀
No. 3 or G. P.‡	———	α Seville	673	B & W	β 673d1	724	1–30–20	B & W	♀
G. P.	R & W	α Ellen	651	B & W	β 651s2	—	3–23–20	B & W	♂
G. P.	R & W	α Daisy	661	B & W	β 661s3	—	3–30–20	B & W	♂
G. P.	R & W	Hailey Segis Judy Colantha Univ. of Ill. Herd No	190082 632	B & W	632d1	—	4– 1–20	B & W	♀
G. P.	R & W	α Jane	654	B & W	β 654s3	—	4– 3–20	B & W	♂
G. P.	R & W	α Dora	656	B & W	β 656s1	—	5– 2–20	B & W	♂
G. P.	R & W	α Blackfoot	653	B & W	β 653s4	—	6– 1–20	R & W	♂
No. 3	B & W	β No. 1	708	R & W	708s1	—	7– 2–20	R & W	♂
No. 3	B & W	β 21	709	R & W	709d1	—	7–14–20	B & W	♀
No. 3	B & W	α Emma	666	B & W	β 666d2	—	9–28–20	R & W	♀
No. 3	B & W	α Twisk	657	B & W	β 657d3	—	9–30–20	B & W	♀
G. P.	R & W	Hailey Segis Katherine Univ. of Ill. Herd No	188895 634	B & W	634s3	—	10–11–20	B & W	♂
No. 3	B & W	α Faniel	662	B & W	β 662d3	—	10–12–20	B & W	♀
No. 3	B & W	β Rosy	705	R & W	705d2	—	10–21–20	B & W	♀
No. 3	B & W	α Emerald	663	B & W	β 663d1	—	11– 2–20	B & W	♀

‡Cow No. 724 was carried in dam at the time the herd was purchased by the UNIVERSITY OF ILLINOIS. The breeding records furnished by the BOWLKER estate do not give a date of service for α Seville, No. 673, during 1919. The only bulls in service at the time this cow must have been served were No. 3 and Guernstein Prince. Consequently, they are given as the sire. No. 724 is being mated with red bulls and if she drops all black calves it will be assumed that she is homozygous and must have been sired by the black bull No. 3. If she drops red calves it will be assumed that she is heterozygous and may have been sired by either No. 3 or Guernstein Prince.

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Bowlker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
No. 3	B & W	α Fannie	655	B & W	β 655d2	—	11–13–20	B & W	♀
No. 3	B & W	α Annie	670	B & W	β 670d1	—	11–20–20	B & W	♀
No. 3	B & W	β Dorise	702	R & W	702s1	—	11–26–20	R & W	♂
No. 3	B & W	α Sylvene	665	B & W	β 665d3	—	12–25–20	B & W	♀
No. 3	B & W	α Katha	680	B & W	β 680s1	—	12–31–20	B & W	♂
G. P.	R & W	Holfecta	668	B & W	668d2	—	1– 1–21	B & W	♀
No. 3	B & W	β 18	711	B & W	711d1	—	1– 3–21	B & W	♀
No. 3	B & W	β Dora	707	B & W	707d1	—	1– 3–21	B & W	♀
No. 3	B & W	β 11	712	B & W	712s1	—	1– 4–21	B & W	♂
No. 3	B & W	β 38	713	B & W	713s1	—	1–16–21	B & W	♂
G. P.	R & W	Guernlady	667	R & W	667s1	—	1–29–21	R & W	♂
No. 3	B & W	α Seville	673	B & W	β 673d2	—	1–30–21	B & W	♀
No. 3	B & W	α Maid	682	B & W	β 682d1	—	2– 3–21	B & W	♀
No. 3	B & W	α Theresia	687	B & W	β 687s1	—	2– 9–21	R & W	♂
No. 3	B & W	α Kate	652	B & W	β 652d1	—	2–10–21	R & W	♀
No. 3	B & W	β 24	714	R & W	714d1	—	3–12–21	B & W	♀
O. C. H.	B & W	β 50	717	B & W	717s1	—	6–17–21	B & W	♂
No. 3	B & W	α No. 5	683	B & W	β 683s2	—	7–15–21	B & W	♂
J. M. K. Y	R & W	Hailey Segis Judy Colantha Univ. of Ill. Herd No	190082 632	B & W	α 632d2	—	7–28–21	B & W	♀
O. C. H.	B & W	β 55	720	R & W	720d1	—	8–29–21	B & W	♀
G. P.	R & W	α Colerie	674	R & W	β 674d2	—	9– 3–21	R & W	♀
O. C. H.	B & W	β 58	721	B & W	721d1		9–21–21	B & W	♀
G. P.	R & W	α Emerald	663	B & W	β 663s2	—	11–19–21	R & W	♂
No. 3	B & W	α Annie	670	B & W	β 670d2	—	12– 4–21	B & W	♀
No. 3	B & W	α Twisk	657	B & W	β 657d4	—	1–16–22	B & W	♀
O. C. H.	B & W	β Rosy	705	R & W	705d3	—	1–16–22	B & W	♀

TABLE 6 (continued)

Breeding, date of birth, color and sex of animals born in Boulker hybrid herd previous to November 8, 1922.

MALE PARENT		FEMALE PARENT			ORIGINAL NAME OR NUMBER	UNIVERSITY OF ILLINOIS HERD NUMBER	DATE OF BIRTH	COLOR	SEX
Name	Color	Name	Number	Color					
O. C. H.	B & W	β Dora	707	B & W	707s1	—	1–16–22	B & W	♂
No. 3	B & W	α Fannie	655	B & W	β 655d3	—	1–21–22	B & W	♀
No. 3	B & W	α Seville	673	B & W	β 673d3	—	1–24–22	B & W	♀
No. 3	B & W	α Seville	673	B & W	β 673s1	—	1–24–22	B & W	♂
G. P.	R & W	α Elizabeth	689	B & W	β 689d1	—	2–12–22	R & W	♀
No. 3	B & W	α Sylvene	665	B & W	β 665d4	—	2–14–22	R & W	♀
G. P.	R & W	Guernlady	667	R & W	667s2	—	3– 1–22	———	♂
O. C. H.	B & W	β Dorise	702	R & W	702d1	—	3–10–22	B & W	♀
O. C. H.	B & W	β 24	714	R & W	714d2	—	3–29–22	B & W	♀
O. C. H.	B & W	Hailey Gloria Univ. of Ill. Herd No	40784 636	R & W	α 636d1	—	4–14–22	B & W	♀
O. C. H.	B & W	β 39	715	R & W	715d1	—	5–15–22	B & W	♀
No. 3	B & W	α No. 5	683	B & W	β 683d2	—	7– 3–22	R & W	♀
G. P.	R & W	α Jane	654	B & W	β 654s4	—	8– 1–22	R & W	♂
I. V. K.	R & W	β 34	710	R & W	710d1	—	10– 1–22	R & W	♀
I. J. O.	B & W	632d	648	B & W	648s1	—	10–14–22	B & W	♂
No. 3	B & W	α Blackfoot	653	B & W	β 653s5	—	10–18–22	B & W	♂
I. V. K.	R & W	β 57	718	R & W	718d1	—	10–18–22	R & W	♀
I. V. K.	R & W	Hol-Elliston	671	B & W	671s2	—	10–27–22	B & W	♂
A. V. F. P.	R & W	Hailey Segis Judy Colantha Univ. of Ill. Herd No	190082 632	B & W	α 632d3	—	10– ?–22	B & W	♀
I. V. K.	R & W	673d	724	B & W	724s1	—	11– 1–22	B & W	♂
No. 3	B & W	α Daisy	661	B & W	β 661s4	—	11– 7–22	R & W	♂

PERICARP STUDIES IN MAIZE. II. THE ALLELOMORPHISM OF A SERIES OF FACTORS FOR PERICARP COLOR[1]

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INTRODUCTION

The majority of the pericarp colors found in North American varieties of maize are due to the presence of an orange or brick-red pigment rather insoluble in water. They differ from each other in the amount of pigment present and in its distribution. EMERSON (1911), studying several of these pericarp colors, found that they were not inherited independently; in fact they failed to give any recombinations. He interpreted his results on the basis of complete linkage (coupling and repulsion). The case has since been considered one of multiple allelomorphism of the *P* factor (ANDERSON and EMERSON 1923).

A survey of this series has been made to determine the extent of the series and also to see if any crossing over or recombination takes place between members of the series. The colors and color patterns belonging to this series are numerous and the intensity of color in each type varies with differences in stage of maturity and in rate of maturing. They have been grouped into relatively few classes according to the general color of the pericarp itself and of the cob.

[1] Paper No. 125, Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, New York.

DESCRIPTIONS[2]

RR, red. Both pericarp and cob deep red.

OR, orange. Pericarp light red or orange; cob red or orange. This class includes several members differing in intensity of color.

WR, red-cob white. Pericarp white (colorless) in some varieties, pale orange in others; cob red. St. Charles White has colorless pericarp with red or light-red cob. Reid's Yellow Dent and Pride of the North sometimes have the basal part of the pericarp colored; ears with streaky coloration in the pericarp are frequent. Some other varieties show a pale orange color throughout the pericarp.

OW, light orange with white cob. Pericarp uniformly pale orange; cob white or pale. This class includes EMERSON's "Bronze Pop" (ANDERSON 1921) and "light brown" (EMERSON 1911), and HAYES's "Pattern" (HAYES 1917). These have not been used in the following tests because their heterozygous forms are so pale that their separation from white is difficult unless the plants are very well matured.

CW, white-cap. Pericarp red or orange at base and sides, gradually fading out to white at tip of grain; cob white. Northwestern Dent.

CR, Red-cob white-cap. Pericarp like the preceding; cob red.

WW, white. Pericarp and cob white (colorless).

VV, variegated. Variegated pericarp and cob. A series of types grading from almost entirely white to strongly variegated with red. They are highly mutable, throwing red, white and a series of light-, medium-, and strongly variegated types. This series has been described and figured by EMERSON (1914, 1917). Calico Dent.

MO, mosaic. Another series of mutable types resembling variegated in general appearance. Crown patch (at tip of grain) and cob light-colored or white. Mutable, throwing darker and lighter mosaics and white. Red occurs only rarely by mutation. This series has been described and figured by HAYES (1917). Brindle Flint.

DOMINANCE

In general, color in any portion of the pericarp or cob is dominant to white (colorless) and the deeper reds are dominant to the lighter ones. Dominance is, however, not complete. The less deeply-colored types (OR, OW, CR, CW), crossed with white, give F_1 hybrids lighter in color, but with the color distributed in the same pattern as in the colored parent.

[2] The symbols used in this paper refer to the color types or classes. In general, the first letter refers to the pericarp color, the second to the cob color. The factors responsible may be symbolized as allelomorphs of P by using the same letters as superscripts as P^{rr} P^{or}, P^{wr} P^{ow}, etc.

Red and variegated show but little reduction in color due to heterozygosis with white. In these types the amount of pigment is so great that a considerable decrease in quantity would have but little effect on the appearance.

When types showing color in different regions are crossed, both regions are colored in the hybrid. Thus, in the cross WP×VV, the hybrid has a red cob and variegated pericarp. The hybrid CW×VV shows the CW pattern in light-red overlaid by deep-red variegation.

TESTS FOR ALLELOMORPHISM

The tests reported here were made by crossing two different types and out-crossing the hybrid with a white-pericarp strain. Independent inheritance should give four classes in equal numbers; the combination type (like the F_1), the two parental types, and white. Allelomorphism or complete linkage should give only two classes, the two parental types. Incomplete linkage should give mainly the two parental types, the cross-overs appearing as the combination type and white.

A small amount of error is expected due to accidental stray pollination. Such stray pollination may give plants resembling the pistillate parent but cannot give the alternative class. At most, the error should be only a very small fraction of one percent.

Most of the white-pericarp plants used in the out-crosses were derived from intercrosses of Sanford's White (flint), a medium-early white dent and two early pop-like strains from Doctor EMERSON'S cultures.

Crosses between stable types

WR×CW. Table 1 gives the results of tests for allelomorphism of the factors for red-cob white and white-cap. Only the two parental types were obtained. There were 1751 red-cob white plants, 1684 white-cap. This cross is not wholly satisfactory, since heterozygous CW is light-colored, making immature ears difficult to separate from white. No red-cobbed ears showed the CW pattern, whereas all well-matured white-cobbed ears showed this pattern distinctly.

WR×RR. Similar tests involving red-cob white and red gave 1001 red-cob white, 993 red and 1 variegated. Occasional variegated ears are expected as mutations from red. This test does not give evidence on the combination class, due to the dominance of red. White ears would have been detected if present.

TABLE 1

Progeny of the hybrid WR×CW out-crossed to WW.

PEDIGREE NUMBERS	WR	CW
542	112	105
543	42	44
544	31	38
545	66	71
546	77	79
548	150	152
550	35	37
551	177	149
554	139	145
555	122	109
1702	179	158
1703	208	188
1704	117	118
1735	219	210
1767	77	81
Total	1751	1684

TABLE 2

Progeny of the hybrid WR×RR out-crossed to WW.

PEDIGREE NUMBERS	WR	RR	VV
533	155	170	..
534	134	125	..
535	21	22	..
536	70	78	..
537	146	122	..
538	130	114	..
539	150	158	1
1501	106	112	..
1502	89	92	..
Total	1001	993	1

CW×RR. In tests involving the white-cap and red types, 1149 plants were white-cap and 1227 were red. Many plants were immature, making white-cap difficult to distinguish from white. If cob color and pericarp color were due to separate but closely linked factors, crossovers would be detected in this test.

TABLE 3

Progeny of the hybrid CW×RR out-crossed to WW.

PEDIGREE NUMBERS	CW	RR
566	206	221
1503	85	83
1504	78	87
1505	50	52
1522	147	162
1523	95	131
1524	137	137
1525	148	172
1526	89	85
1527	114	97
Total	1149	1227

Crosses involving variegated

For tests involving variegated, red-cob white is of greatest value, as it is easily separated from the mutation products of variegated. Red-cob white-cap is second in value. In all tests with variegated a small number of reds and whites are expected by mutation.

WR×VV. Tests for allelomorphism of the factors for red-cob white and variegated have given 2374 red-cob white, 2246 variegated, 70 red

TABLE 4

Progeny of the hybrid WR×VV out-crossed to WW.

PEDIGREE NUMBER	WR	VV	RR	WW
454	243	229	25	1
501	192	179	12	1
502	152	154	1	..
503	270	263	..	1
579	146	167	5	1
1686	185	168	5	..
1691	107	104	..	..
508	186	193	5	..
509	157	124	1	3
510	92	76	3	..
512	76	51	1	1
513	133	126	7	3
514	62	56	2	1
515	120	117	1	1
1770	138	118	1	..
1772	115	121	1	2
Total	2374	2246	70	15

and 15 white (table 4). No combination-type ears (red-cob variegated) were obtained. The presence of white ears by mutation would prevent the detection of whites by crossing over if any such occurred.

OR×VV. For this test a medium-orange with red cob was used. When heterozygous the cob was red and the pericarp frequently very pale. There were obtained 773 red-cob light-orange ears, 712 variegated, 26 red and 4 white (table 5). Again no combination-type ears appeared. Tests with deep-orange were carried out with smaller numbers, but the difficulty of making separations makes the data of much less value.

TABLE 5

Progeny of the hybrid OR×VV out-crossed to WW.

PEDIGREE NUMBER	OR	VV	RR	WW
517	132	121	4	1
518	142	119	12	..
520	101	74	1	1
522	137	137	2	..
523	124	126	5	..
516	137	135	2	2
Total	773	712	26	4

CR×VV. Tests involving red-cob white-cap and variegated gave 714 CR, 683 VV and 14RR (table 6). In addition one combination-type (CR+VV) ear appeared, which may have been due to crossing over or to stray pollination, the F_1 having been used as pistillate parent. The seeds had been killed by freezing before maturity, so no progeny tests could be made.

TABLE 6

Progeny of the hybrid CR×VV out-crossed to WW.

PEDIGREE NUMBER	CR	VV	RR
1740*	92	97	1
1743	103	106	2
1746	113	109	5
1747	74	71	..
1751	120	111	3
1754	111	105	1
1760	101	84	2
Total	714	683	14

*Also one combination type (CR+VV).

CW×VV. Tests with white-cap proved unsatisfactory, due to immaturity and the paleness of the pericarp color in heterozygous white-cap ears. One ear was obtained which was apparently of the combination type, CW+VV. Like the one in the preceding test, it may have been due either to crossing over or to stray pollination, the F_1 having been used as pistillate parent. It also was frozen before maturity.

RR×VV. This test gave 1399 red, 1308 variegated and 2 white (table 7). The red class includes the red mutations from variegated. As neither recombination class could be separated from other types present, a small amount of crossing over would not have been detected.

TABLE 7

Progeny of the hybrid RR×VV out-crossed to WW.

PEDIGREE NUMBER	RR	VV	WW
567	98	87	..
568	79	81	..
1506	98	94	..
1507	46	41	..
1509	133	112	2
1510	131	112	..
1511	72	83	..
1512	54	58	..
1514	66	59	..
1516	120	104	..
1517	78	70	..
1518	92	86	..
1519	87	86	..
1520	119	109	..
1521	126	126	..
Total	1399	1308	2

Crosses involving mosaic

HAYES (1917) concluded from studies on mosaic pericarp color that mosaic, self-red, "pattern," and colorless form a series of allelomorphic types. Through the kindness of Professor HAYES, the writer has been enabled to compare both his mosaic and his self-red with other types. "Pattern" proved so light-colored in heterozygous combination with white, especially in immature ears, that no significant results were obtained with it. The self-red appears to be identical with reds obtained from other sources and has been used interchangeably with them. The results with mosaic are in accord with those obtained by HAYES, except

that crosses between mosaic and self-red have given self-red instead of intermediates when grown under field conditions at Ithaca, New York.

The data in the following tables show that mosaic is included in the same series as the other types presented in this paper. A few reds occur, which are presumably mutations from mosaic. Some of the light mutations from mosaic were nearly white, a few perhaps entirely white, so that white crossovers if present would not have been detected. Table 8 gives the results of tests for allelomorphism of red-cob white and mosaic. Table 9 gives similar data on tests of orange and mosaic. No combination-type ears were present in either lot. Table 10 gives the results of tests with white-cap and mosaic. These data are not very satisfactory, since

TABLE 8

Progeny of the hybrid WR×MO out-crossed to WW.

PEDIGREE NUMBER	WR	MO	RR
1551	116	119	..
1556	143	135	1
1562	138	144	..
1597	163	139	1
1601	23	26	..
1603	128	142	..
1607	159	170	..
1644	106	106	..
1648	129	125	1
1653	74	85	..
1658	118	120	..
1663	73	73	..
1668	139	124	..
Total	1509	1508	3

TABLE 9

Progeny of the hybrid OR×MO out-crossed to WW.

PEDIGREE NUMBER	OR	MO	RR
1581	48	45	..
1592	106	98	..
1593	62	49	..
1594	98	87	..
1638	128	106	..
1640	146	166	1
Total	588	551	1

the combination type is not easily detected except on well-matured ears. No combination-type ears were observed. Table 11 gives the results of tests with red and mosaic, giving, as expected, only red and mosaic ears.

TABLE 10

Progeny of the hybrids CW×MO out-crossed to WW.

PEDIGREE NUMBER	CW	MO	RR
1565	139	138	..
1569	70	53	1
1570	79	81	..
1572	124	131	..
1574	118	118	..
1579	30	25	..
1583	77	77	..
1584	63	47	..
1586	127	123	..
1588	148	149	..
1615	114	94	1
1617	40	45	..
1618	51	53	..
1621	60	55	..
1624	32	32	3
1626	99	109	..
1630	72	68	..
1633	154	132	..
1635	66	42	..
Total	1663	1572	5

TABLE 11

Progeny of the hybrid RR×MO out-crossed to WW.

PEDIGREE NUMBER	RR	MO
1531	29	35
1533	19	15
1534	81	54
1536	3	5
1537	32	52
1540	9	13
Total	173	174

ALLELOMORPHISM *versus* LINKAGE

The more obvious lines of evidence bearing on this question may be summarized as follows:

1. Data from the tests reported. No case of crossing over or recombination was found where the tests were critical and not subject to other interpretations. Two combination-type ears appeared which may have been due to crossing over or more probably to stray pollination. Unfortunately these exceptional ears could not be tested as they were frozen before reaching maturity. The evidence is strongly in favor of complete linkage or allelomorphism. The other genes in the same linkage group, those for tassel seed, brachytic culms and fine striping, give about one, thirty-seven, and thirty-five percent of crossing over, respectively, with genes for pericarp color (ANDERSON and EMERSON 1923).

2. New types such as might occur from crossing over have not been observed in progenies resulting from crosses of different pericarp types. The only new types found are those which are known to occur by mutation in the variegated and mosaic series. Red-cob variegated, such as is obtained in the F_1 of WR×VV, has never bred true and no varieties of this type have been found.

The evidence here also favors allelomorphism or complete linkage. But the evidence does not contribute to the distinction between allelomorphism and complete linkage of non-allelomorphic genes. By allelomorphism is meant the actual homology of genes; by complete linkage, the failure of non-homologous genes to show crossing over.

3. New types occurring repeatedly in the variegated and mosaic series behave as allelomorphs of the genes from which they were derived. Crossing over is here out of the question, as the mutations may occur in any somatic cell. Synchronous mutation of a group of genes is far less probable than mutation of a single gene. This evidence is strongly in favor of allelomorphism as opposed to linkage, either complete or incomplete.

NUMBER OF ALLELOMORPHS AND THEIR ARRANGEMENT IN SERIES

The total number of distinct genes included in this allelomorphic series is much greater than the number of classes given on page 443. Most of the classes include several heritably different colors or color patterns. All red-cob types were included in the class WR if the pericarp was so light-colored when heterozygous with white, that it could not readily be separated from a standard red-cob white. All that were fully red in both homozygous and heterozygous condition were designated as red. All that were distinctly intermediate in pericarp color and either red or intermediate in cob color were classified as orange. Only strains which appeared to be free from pericarp color were classified as white. All white-

cob strains showing color in the pericarp were classified as OW if the color was uniformly distributed over the pericarp or as CW if the pericarp was white-capped. Only the type CR was represented by a single strain. No attempt was made to establish the allelomorphism of the different grades included in the same class. It was observed, however, that in general the type recovered from a cross resembled closely the parental type.

These allelomorphic genes can be arranged in several series. A series can be formed from the deepest red through orange and light-orange to white. A similar series can be formed from red through orange with red cob (included in OR) and red-cob with pale-orange pericarp (included in WR) to a red-cob white which has no color in its pericarp. The existence of different intensities of cob color in such red-cob white varieties as St. Charles White suggests a series grading from a deep-red cob to pure white. However, no data are available on this point. Several other series may also be formed, but no one simple series can be formed to include all types.

The variegated and mosaic classes are even more complex, and each can be separated into a series based on the amount of color in the pericarp or on the frequency of mutation. EMERSON (1913, 1917) has shown for variegated (VV) that a series of allelomorphs can be formed to include white, light-variegated, medium-variegated, dark-variegated and red. These divisions are arbitrary, for as many grades can be selected as one chooses to work with. HAYES (1917) has shown a somewhat similar series for mosaic. These mutable types are unique in that they can generate very quickly a complete graded series of allelomorphs.

Since the known varieties of maize are numerous and the pericarp and cob colors are capable of such diverse modifications, it is not surprising to find a very large number of allelomorphs. The varieties and strains as yet unknown or untested are even more numerous. Doubtless this series will be greatly enriched by future acquisitions.

SUMMARY

A large series of pericarp color types in maize has been shown to be allelomorphic or closely linked in inheritance.

The evidence is believed to be in favor of allelomorphism because:

1. Tests have given no clear evidence of crossing over.
2. In progenies of crosses of different pericarp types, parental types only have been observed to breed true.

3. Inherited somatic mutation is more easily interpreted as resulting from modifications of single genes.

An undetermined but large number of genes are involved in this series. Two series of highly mutable genes are included

The genes in this allelomorphic series can not be arranged in any simple graded series. Rather, they group themselves into several diverse series.

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CHROMOSOME BEHAVIOR IN A GENUS CROSS[1]*

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Crosses between different genera of plants are rare and a satisfactory cytological study of such hybrids has never been made. A comparison of chromosome behavior in genus and species crosses is of interest in connection with a comparison of genetic and taxonomic relationships. A cytological analysis should also show the reason why crosses of genera are almost completely or quite sterile and whether there is any possibility of obtaining fertile progeny.

Crosses were made between *Aegilops cylindrica* Host. and *Triticum vulgare* Vill. var. *lutescens* Korn., agronomic variety Marquis. *Aegilops cylindrica* is a wild grass distributed in Italy, the Balkans, South Russia and Asia Minor (PERCIVAL 1921). The culms are hollow and thin-walled and the outer glumes are rounded on the back. The rachis does not disarticulate into separate spikelets, as is the case in certain wild wheats, but is brittle as in *T. Spelta*. The terminal spikelets bear one or two long awns.

Marquis is one of the most important varieties of *T. vulgare*. It is an awnless spring wheat of high quality. The culms are 95 to 115 cm tall, which is about twice the height of the culms of *Aegilops cylindrica*. The heads of the two parents and the F_1 hybrid are shown in plate 1. This photograph was obtained from Doctor E. F. GAINES, who happened to have the same hybrid in his experimental plots at WASHINGTON STATE COLLEGE.

The cross of these two genera resulted in several seeds. These were planted in the greenhouse at BUSSEY INSTITUTION in the fall of 1921. Two F_1 plants were obtained. These plants were unusually vigorous in vegetative development, but were completely sterile. The sterility of the F_1 was also indicated by the appearance of the pollen grains which were obviously imperfect with very few exceptions. The F_1 plants were more or less intermediate in appearance. Doctor GAINES has recently

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[1] Papers from the Biological Laboratory, MAINE AGRICULTURAL EXPERIMENT STATION, No. 162.

made numerous crosses of *Aegilops cylindrica* with several Vulgare wheats and in some crosses about 2 percent of the spikelets set seed.

BELLING'S (1921) method was used to obtain chromosome counts of the parents. *Aegilops cylindrica* has 14 haploid chromosomes and *T. vulgare* has 21 haploid chromosomes. These counts were checked with root-tip preparations of Aegilops and sectioned anthers of Marquis wheat (SAX 1922). Camera lucida outlines of the chromosomes in the reduction of the pollen mother cells are shown in plate 1,a.

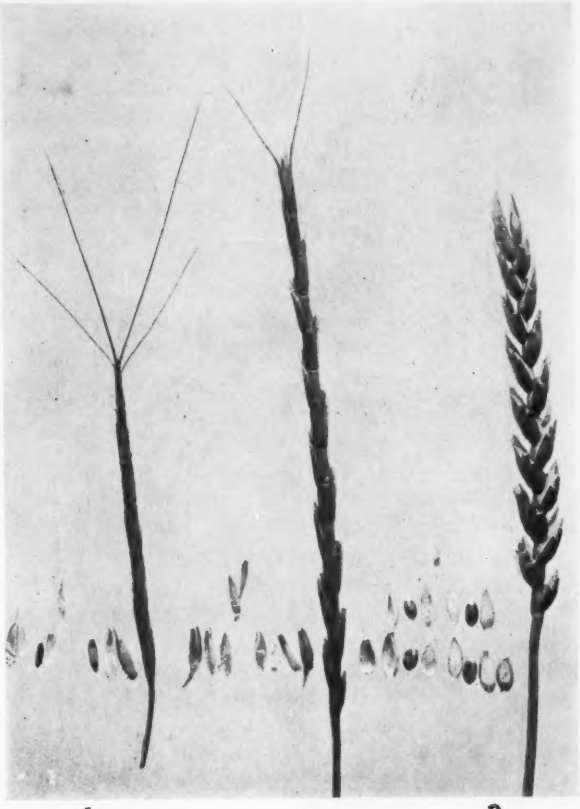
The F_1 anthers were fixed in a modified Bouin's solution (ALLEN 1916). The material could not be washed and dehydrated at the time, so the anthers were left in the fixing solution almost a year. It was surprising to find that the fixation was unusually good and many excellent preparations were obtained. Sections were cut 10μ to 12μ thick and stained with Haidenhain's iron-haematoxylin. The drawings were done in ink and in all cases were from single sections.

The F_1 plant receives 14 chromosomes from Aegilops and 21 chromosomes from the wheat parent. Thus, there should be 35 chromosomes in the somatic cells of the F_1 plant. In species crosses of wheat with the same parental chromosome numbers there are 14 bivalents and 7 univalents in the first reduction division (SAX 1922). One might expect a similar behavior in this genus cross, but such is not the case. At the time of diakinesis in the pollen mother cells there are both paired and unpaired chromosomes, but the number of each cannot be accurately counted at this stage (plate 2, 1). In the metaphase of the first reduction division the bivalents and univalents can be easily distinguished. There are 6 or 7 bivalents surrounded by about 21 univalents. Polar views of the metaphase are shown in plate 2, figures 2, 3 and 4. The grouping of the bivalents surrounded by the univalents is typical and the contrast is made more striking due to the greater size and deeper staining capacity of the bivalents. The number of bivalents is usually 7, but occasionally only 5 or 6 could be identified. The number of single chromosomes that could be counted was often less than 21, but since some of these univalents are frequently at either pole during the metaphase, they may be in adjacent sections or may not be so readily detected. Some of the univalents may not become oriented on the equatorial plate, as shown in plate 2, 5. This behavior is typical, although occasionally the univalents are all on or near the equatorial plate, as shown in plate 2, 6.

Several cases were found where the univalents had lagged behind and divided equationally. In plate 2, 7 there are about 16 lagging univalents which have divided. The lagging univalents can be easily distinguished

DESCRIPTION OF PLATE 1

FIGURE 1.—*Aegilops cylindrica.*
FIGURE 2.—*Aegilops cylindrica* × *Triticum vulgare* F_1.
FIGURE 3.—*Triticum vulgare* (Marquis).
FIGURE *a*.—Chromosomes of *Aegilops cylindrica* at the time of reduction of pollen mother cells.
FIGURE *b*.—Chromosomes of Marquis wheat at same stage.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b

from the bivalents because of their size and method of dividing. In most cases, however, the 21 univalents apparently remain at the poles or pass to the poles without dividing. At the telophase there are no chromosomes left on the equatorial plate, but occasionally there appears to be some disintegrating chromatic material in the cytoplasm. A typical case is shown in plate 2, 8. In later stages, however, there are seldom any chromosome fragments or extra nuclei to be found.

The chromosome counts in the metaphase of the second division indicate that the univalents frequently pass to the poles without dividing in the heterotypic division. If the univalents pass to either pole at random there would be from 7 to 28 chromosomes at either pole, but usually (in 81 percent of the cases) 15 to 20. We do find about 17 or 18 chromosomes in the metaphase of the second division in plate 2, 9, and similar counts were obtained in other diads. In the second division there is some lagging of chromosomes in the anaphase, but in most cases the division is comparatively regular (plate 2, figures 10 and 11). If the univalents divide in the first division it is probable that they lag behind and do not divide in the second, while if they do not divide in the first division they will probably divide normally in the second division. Whether the 21 univalent chromosomes divide in the first or second division makes but little difference if they divide but once, as occurs in similar cases in other crosses. In a few cases extra nuclei were formed, but as a rule the second division is regular and normal tetrads are formed (plate 2, figure 12).

DISCUSSION

When species which differ in chromosome number are crossed, the behavior of the chromosomes in the reduction divisions of the F_1 plant varies greatly in different crosses. The behavior of chromosomes in certain species crosses is of interest in comparison with chromosome behavior in the genus cross. The following illustrations indicate the great variability in chromosome behavior in different species hybrids.

1. All chromosomes of the F_1 may fail to pair. *Crepis setosa*, with 4 haploid chromosomes, crossed with *C. capillaris*, with 3 haploid chromosomes, produced an F_1 with 7 chromosomes in the somatic cells. In the reduction division of the F_1 there is no pairing of the chromosomes. The division is irregular and usually the chromosomes pass into the poles without dividing. The F_1 is partially sterile (COLLINS and MANN 1923).

2. A varying number of parental chromosomes may pair in the F_1 reduction division. When *Polypodium aureum* with $34\pm$ chromosomes is crossed with *P. vulgare*, var. *elegantissimum*, which has $90\pm$ chromosomes,

DESCRIPTION OF PLATE 2

Preparations from pollen mother cells of the F_1 of *Aegilops cylindrica*×*Triticum vulgare*. All drawings were made from single sections. Magnification 750 diameters. No reduction.

FIGURE 1.—Paired and unpaired chromosomes in diakinesis.

FIGURE 2.—Polar view of metaphase of heterotypic division. 7 bivalents and 21 univalents.

FIGURE 3.—Heterotypic division with 7 bivalents and 19 univalents.

FIGURE 4.—Heterotypic division with about 6 bivalents and 21 univalents.

FIGURE 5.—Side view of metaphase of heterotypic division showing distribution of bivalents and univalents

FIGURE 6.—Same as 5 but univalents grouped.

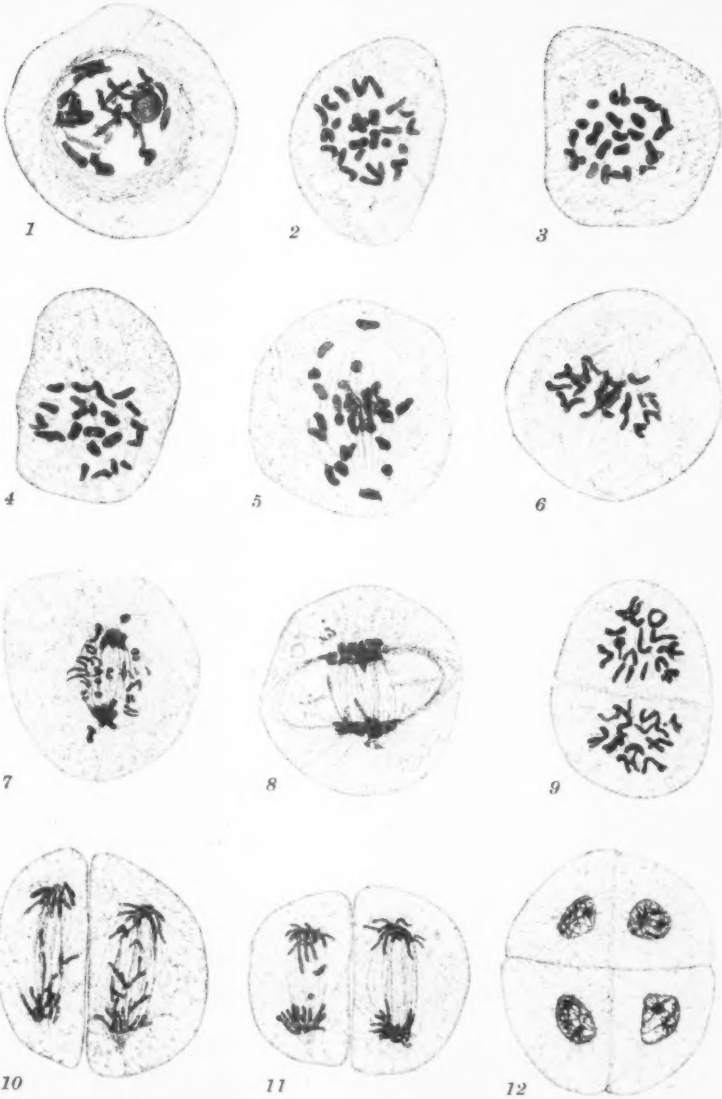
FIGURE 7.—Division of the lagging univalents.

FIGURE 8.—Telophase of heterotypic division.

FIGURE 9.—Metaphase of second division with about 18 chromosomes on each equatorial plate.

FIGURES 10,11.—Late anaphase and telophase of homeotypic division.

FIGURE 12.—Normal tetrad.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an F_1 plant is produced which has $124\pm$ somatic chromosomes. In the first reduction division there are 95 to 125 chromosomes, indicating that a varying number of the parental chromosomes pair. The division is irregular and the F_1 is quite sterile (FARMER and DIGBY 1910).

3. All chromosomes of one parent may pair with some of the chromosomes of the other parent. In crosses of 2 species of Drosera with 10 and 20 chromosomes, respectively, the 10 chromosomes of one parent pair with 10 of the other parent, leaving 10 single chromosomes (ROSENBERG 1909). In rose hybrids bivalents and univalents are found in multiples of 7. Certain hybrids have 7 bivalents and 7, 14, 21 or 28 univalents (BLACKBURN and HARRISON 1921, TÄCKHOLM 1922). In crosses of *Triticum durum* or *T. polonicum* with *T. vulgare* the 14 chromosomes of *T. durum* pair with 14 chromosomes of *T. vulgare*, leaving 7 single *vulgare* chromosomes (KIHARA 1919, SAX 1922). The bivalents divide normally but the univalents are irregularly distributed. Various degrees of sterility occur in the F_1 of such hybrids.

4. The chromosomes contributed by one parent may not pair with those of the other parent, but pairing may occur among the chromosomes contributed by only one of the parents. This method of chromosome behavior is found in crosses of *Crepis setosa* ($n=4$) with *C. biennis* ($n=20$). In the F_1 meiosis the 20 *biennis* chromosomes pair with each other while the 4 *setosa* chromosomes remain unpaired. The divisions of the pollen mother cells are comparatively regular.

5. All of the chromosomes may pair, even when one or two extra sets of chromosomes are present. In triploid Daturas there are 36 somatic chromosomes. In the first reduction division the chromosomes are grouped in 12 sets of 3 chromosomes each. In the first division of the pollen mother cells 2 chromosomes of each set go to one pole and the remaining chromosome goes to the other pole. In tetraploid plants the chromosomes unite in groups of four (BELLING and BLAKESLEE 1923). The triploid plants are partially sterile but tetraploids are almost completely fertile.

The behavior of the chromosomes in the genus cross of Aegilops $\times$ Triticum does not differ greatly from the behavior in certain species crosses. In this cross 7 Aegilops chromosomes presumably pair with 7 wheat chromosomes, leaving 21 single chromosomes, 7 of which are from Aegilops and 14 from the wheat parent. The bivalents divide normally, but the univalents are apparently distributed at random without dividing in one of the reduction divisions. The discussion of chromosome behavior in the cross of Aegilops $\times$ *T. vulgare* will be based on the

typical chromosome behavior for calculating chromosome recombinations.

Sterility in these crosses can be attributed to the incompatibility of certain chromosomes and to differences in parental chromosome number which results in univalent chromosomes at the time of the reduction divisions in the F_1 hybrids. In certain cases at least the gametic and somatic perfection increases as the chromosome number approaches some multiple of a basic chromosome number. In Triticum and Rosa this number is 7. The random distribution of univalents results in a frequency distribution of gametic chromosome numbers in which the parental numbers, or numbers which are a multiple of the basic number, are seldom recovered.

In the F_1 hybrid of *Triticum durum* × *T. vulgare* it was assumed that the 14 chromosomes of the *durum* parent paired with 14 of the 21 *vulgare* chromosomes. This assumption is based on the fact that in general the maternal and paternal chromosomes pair, and on the genetic behavior of F_2 segregates. *Crepis biennis* with 20 chromosomes does not differ greatly from certain species with 4 or 5 chromosomes. Back-crosses of *C. setosa* × *C. biennis* with *biennis* give segregates with 10 *biennis* chromosomes and the *biennis* type of plants (COLLINS and MANN 1922). In view of these facts it is not improbable that *biennis* contains 4 similar sets of chromosomes. In wheat, on the other hand, the species with 7, 14 and 21 chromosomes differ greatly in taxonomic, ecological and economic characters (SAX 1923). A study of crosses between the 14- and 21-chromosome groups shows that the 7 *vulgare* chromosomes which do not pair in the reduction division of the F_1 plant, determine the typical *vulgare* characters and are therefore probably different in genetic constitution from the 14 *vulgare* chromosomes which pair. It is possible, however, that the *vulgare* characters are due simply to duplication of hereditary factors. The fact that all 14-chromosome segregates in F_2 are of the Emmer type would indicate that the 14 *vulgare* chromosomes which pair are similar to the 14 *durum* chromosomes and would therefore be expected to pair with them.

The assumption that sets of chromosomes in wheat do not pair with each other is substantiated by the chromosome behavior in the cross of Aegilops × *T. vulgare*. In this cross there are 21 single chromosomes, 14 of which must be from one of the two parents, whether the 7 bivalents consist of 7 Aegilops and 7 wheat chromosomes or consist of 2 sets of wheat chromosomes.

The sterility of the F_1 hybrid between *Aegilops cylindrica* × *Triticum vulgare* can probably be attributed to chromosome incompatibility

and to the irregular behavior of the chromosomes in the reduction divisions. If the 21 univalents pass at random to one pole or the other, according to the laws of chance, then the F_1 gametes will contain from 7 to 28 chromosomes. In hybrids of wheat species with different chromosome numbers the gametes with an intermediate chromosome number are more or less sterile and the functional gametes have a chromosome number which approaches a multiple of 7. If all gametes with chromosome numbers in multiples of 7 survive in the Aegilops × *T. vulgare* cross, then there would be 1 functional gamete in 2,097,152 with 7 chromosomes, 1 in 18 with 14 chromosomes, 1 in 18 with 21 chromosomes, and 1 in 2,097,152 with 28 chromosomes. However, there is reason to believe that each one of the sets of 7 chromosomes may consist of specific chromosomes which cannot usually be interchanged with those of another set. The chance of getting only the 7 chromosomes of any one set at one pole is only 1 in 38,760 times. Evidently there would be little chance of obtaining functional gametes if only the above combinations survive. The fact that a few seeds are obtained in certain Aegilops × wheat crosses would indicate that functional chromosome combinations are not entirely confined to the above limitations. It will be of interest to follow the chromosome behavior in these F_2 segregates.

If single chromosomes are assorted at random, it is theoretically possible in this genus cross to get a segregate with a chromosome number greater than that of either parent. The union of two 28 chromosome gametes would result in an octoploid species. In the wheat species there is in general an increase in adaptability and economic value as the chromosome number increases from 7 to 21. A new species with 28 chromosomes might be of even greater value than existing varieties.

Although it is improbable that a species with 28 chromosomes would ever be obtained from the cross of Aegilops × *Triticum vulgare*, the possibilities of a similar behavior in other crosses is of interest in connection with the origin of certain wheat species. PERCIVAL (1921) believes that *Triticum vulgare* originated from a cross of Aegilops with a wheat species of the Emmer group. According to PERCIVAL,

> "crossing between mutants of the same specific prototype is, I think, sufficient to account for many, if not all, of the moderate number of forms found among the races of the Emmer series, but the extraordinary complexity and almost endless number of varieties and intermediate forms of the *vulgare* race can only be satisfactorily explained by the assumption of its hybrid origin from two or more distinct species."

The characters which distinguish the Vulgare group from the Emmer group are all found in *Aegilops ovata* and *Aegilops cylindrica*.

Both of the above species of Aegilops have 14 haploid chromosomes. In a cross of Aegilops with a wheat of the Emmer series there would be 28 chromosomes in the somatic cells of the F_1. If 7 Aegilops chromosomes paired with 7 wheat chromosomes, as seems probable from the behavior of chromosomes in the cross of *A. cylindrica* × *T. vulgare*, there would be 7 bivalents and 14 univalents at the time of the reduction division. The random distribution of univalents would result in a 21-chromosome gamete once in 16,384 times. The chances of combining two 21-chromosome gametes are of course rather small. However, in the semi-arid climate of the Mediterranean region cross-pollination probably occurs rather frequently, and in the course of long periods of time such crosses and recombinations might occur which would result in a species of the *vulgare* type. This hypothesis is in accord with the taxonomic, genetic, and cytological relationships of the wheat species and related genera.

The chromosome behavior in the cross of *A. cylindrica* × *T. vulgare* offers an interesting comparison of genetic and taxonomic relationships These two genera differ greatly in morphological characters and in adaptability to climatic conditions. In every respect they seem to merit different generic classification. Certainly the differences are as great as the differences between *T. vulgare* and *Secale cereale*. Although these two genera differ greatly in taxonomic characters they are apparently more closely related genetically than certain species, as indicated by the greater compatibility of the parental chromosomes in F_1 hybrids. In this genus cross 7 chromosomes of Aegilops are apparently compatible with 7 chromosomes of *T. vulgare*. On the other hand a cross of two species of Crepis with 3 and 4 haploid chromosomes, respectively, the chromosomes are so incompatible that the F_1 plant dies at an early stage (BABCOCK and COLLINS 1920). In another cross of Crepis species with 3 and 4 chromosomes, respectively, the F_1 is vigorous but the chromosomes are so incompatible that they do not pair in the reduction division of the pollen mother cells (COLLINS and MANN 1923). These species of Crepis are apparently more similar in taxonomic characters than are *A. cylindrica* and *T. vulgare*, but the chromosomes are more incompatible than in the genus cross. Evidently genus and species classification is not always in accord with chromosome relationships.

SUMMARY

A cross of *Aegilops cylindrica*, a wild grass found in the Mediterranean region, with Marquis wheat, one of the leading varieties of *Triticum vulgare*, resulted in vigorous, but completely sterile, F_1 plants.

Aegilops cylindrica has 14 haploid chromosomes while the wheat variety used has 21 gametic chromosomes. Thus the F_1 plant has 35 chromosomes in the somatic cells. In the first reduction division of the pollen mother cells of the F_1 plant there are about 7 bivalent and 21 univalent chromosomes, due presumably to the pairing of 7 Aegilops chromosomes with 7 wheat chromosomes. If the single chromosomes are distributed at random in the reduction divisions as appears probable, then the chromosome number of the gametes will vary from 7 to 28.

Sterility in this genus cross is due to the incompatibility of certain chromosomes and to chromosome differences in the parents, both of which factors result in univalent chromosomes in the reduction divisions of the F_1 hybrid. With random distribution of the 21 single chromosomes there is little chance of obtaining gametes in multiples of 7. If only gametes with a chromosome number in multiples of 7 survive, as is the case in crosses of wheat species, then most of the sterility can be accounted for. If each set of 7 chromosomes must consist of specific individuals then the chances of recovering fertile gametes are extremely small.

Theoretically, it is possible for a new species with 28 chromosomes to be derived from this genus cross, but the chances for such an occurrence are extremely small.

The behavior of the chromosomes in this cross suggests the possible origin of the *vulgare* wheats from a cross of Aegilops with a wheat species of the Emmer series.

The chromosomes of the two genera, Aegilops and Triticum, are more compatible with each other, as indicated by the number which pair, than the chromosomes of certain species within a given genus.

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THE INHERITANCE OF THE BLOOD GROUPS

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INTRODUCTION

Ever since their discovery in 1900 by LANDSTEINER (1900) and SHATTOCK (1900) working independently, great interest has been shown in the blood groups by medical men. Important research has been carried out on the inheritance of the groups and on their racial distribution, but scarcely more than a paper or two has reached beyond the medical literature. The problems involved are of interest to biologists in general, and to geneticists in particular, so that a summary of our present knowledge of the inheritance of the blood groups should be of value.

The first and most practical application of blood grouping was to the problem of blood transfusion. Prior to the knowledge of blood groups, serious and even fatal reactions often followed the transfusion of blood from one person to another. The knowledge that there were definite substances in the serum of some bloods that would agglutinate, or clump, the red cells of certain other bloods, made possible safe transfusion. By testing the bloods of donor and recipient, no reaction need occur, while in the absence of such tests, serious reactions might occur in approximately a third of the cases (ZIMMERMAN 1920). For safe transfusion, it is only necessary that the serum of the recipient does not agglutinate the red cells of the donor. The principles of blood transfusion have been found to apply equally well to skin grafting (SHAWAN 1919).

At first agglutination was thought to occur only in diseased persons, but it soon became clear that the phenomenon was of general occurrence.

LANDSTEINER (1901) divided human blood into three groups on the basis of the agglutinating reactions. The next year DECASTELLO and

STURLI (1902) described a fourth group. In 1907 JANSKY proposed a definite classification of blood into four groups. Three years later, Moss (1910) in this country, proposed a classification, recognizing, as did JANSKY, four groups. The two classifications differ only in terminology, groups I and IV being interchanged. Both of these classifications were extensively used, causing much confusion and many serious consequences, with the result that a committee was appointed to consider the adoption of a uniform classification. The JANSKY classification, because of its priority, was adopted, and will be used throughout this discussion. The scheme of this grouping is given in table 1.

TABLE 1

Scheme of the JANSKY (1907) *classification of blood groups.*

GROUP	EFFECT OF SERUM	CAPACITY OF CELLS
I	Agglutinates cells of II, III, IV	Not agglutinated by any serum
II	Agglutinates cells of III and IV	Agglutinated by serum of I and III
III	Agglutinates cells of II and IV	Agglutinated by serum of I and II
IV	Does not agglutinate any cells	Agglutinated by serum of I, II, III

These four blood groups have now been shown to occur universally. They have been demonstrated in England (LEARMONTH 1920, KEYNES 1921, DYKE 1922), Germany (VON DUNGERN and HIRSCHFELD 1910), Hungary (VERZÀR 1921-1922), Italy (LATTES 1923), Czechoslovakia (WESZECZKY 1920), Norway (JERVELL 1923), Denmark (JOHANNSEN 1921), Europe in general, including Frenchmen, Bulgarians, Serbians, Greeks, Russians, and Turks (HIRSCHFELD and HIRSCHFELD 1919), China (LIU and WANG 1920), Asia in general (HIRSCHFELD and HIRSCHFELD 1919), Africa (HIRSCHFELD and HIRSCHFELD 1919, PIRIE 1921), Australia (TEBBUT and MCCONNEL 1922), the Philippine Islands (CABRERA and WADE 1921), the United States (HEKTOEN 1907, Moss 1910), and among the Icelanders (JONSSON 1923), the American Indians (COCA and DIEBERT 1923) and the American negroes (LEWIS and HENDERSON 1922). The anthropological importance of the distribution of the groups has been discussed by the HIRSCHFELDS (1919), LEWIS and HENDERSON (1922) and others.

GAY (1907) sought to explain the phenomenon of agglutination on a physico-chemical basis, as due to variations of molecular energy. But it soon became apparent that the clumping must be due to specific substances in the blood. Those in the serum, causing the clumping, were

designated iso-agglutinins, while the receptors in the red cells were called agglutinogens.

To explain the facts of agglutination, Moss (1910) assumed the presence in the blood of three such agglutinins, and three agglutinogens. Other authors (LANDSTEINER 1901, VON DUNGERN and HIRSCHFELD 1910, SCHUTZE 1921) have postulated the presence of only two of each. The latter is the only possible interpretation which will fit all the known facts, as pointed out by UNGER (1921) and GICHNER (1922), and is the one generally accepted at present.

It is also clear from the investigations that the absence of either agglutinogen always coincides with the presence of the corresponding agglutinin. In other words, the agglutinating power of the serum of a blood and the agglutinophilic capacity of its red cells are reciprocal. Moreover, the specific agglutinogens never appear in the offspring unless they are present in the blood of one of the parents, but agglutinins may appear in the offspring, that are absent from the blood of both parents. These facts gave the clue to the possibility of the inheritance of the groups on the basis of two pairs of unit characters, the agglutinogens (now called *A* and *B*) being dominant over their corresponding agglutinins (*a* and *b*).

Interest developed rapidly in the inheritance of the groups. As in most cases of human heredity, studies on the inheritance of blood groups have followed two main lines: first, the collection and interpretation of the available human data; and second, the attempt to learn the blood-group heredity in human beings by observing the behavior of the groups in other forms. The human data will be considered first.

BLOOD-GROUP INHERITANCE IN HUMAN BEINGS

OTTENBERG and EPSTEIN (1908) made the first suggestion that the blood groups might be inherited on a Mendelian basis. VON DUNGERN and HIRSCHFELD (1910), presented data on 72 families, comprising 348 individuals, in which the grouping of the blood had been tested in two generations. The results indicated a probable Mendelian inheritance. In 1916, BREM stated that he found the groups hereditary, and that they probably followed MENDEL'S laws, but he presented no evidence to uphold his view.

No further work was done on the problem until 1920, when LEARMONTH published the results of a study of the blood-group inheritance in forty families in England. From the facts of agglutination as stated above, it was clear that the agglutinophilic capacity was dominant over the power to agglutinate. Proceeding on the assumption, then, that *a* gives the

power to agglutinate *A*, and *b* the power to agglutinate *B*, LEARMONTH (1920) analyzed his forty families, and found that the expectations on a Mendelian basis were fully realized. It is clear that the genetical formulae for the groups, on the JANSKY classification, would be as in table 2.

TABLE 2

Genetic formulae of the four groups.

I	II	III	IV
aabb	*AAbb* *Aabb*	*aaBB* *aaBb*	*AABB* *AaBB* *AABb* *AaBb*

Group IV, being the double dominant, could carry either agglutinin as a recessive. Group I, however, being the double recessive, could not transmit either agglutinogen, and would have to breed true. LEARMONTH'S one exception to the Mendelian rule was found in this connection. Two parents of group I had a child in group II. LEARMONTH suggested illegitimacy as the explanation, and concluded that the groups were inherited as two pairs of Mendelian unit characters.

This conclusion gained ready acceptance among medical men, and received support from several investigators, notable among them OTTENBERG, who was the foremost exponent of the Mendelian inheritance of the blood groups in this country. But it was not destined to escape opposition and criticism, and in 1921-1923 a lively controversy was carried on, chiefly between OTTENBERG (1921, 1922, 1923) and BUCHANAN (1922, 1923) as to the interpretation of the available data. Especially was the medico-legal application of the blood groups the center of a storm of discussion. OTTENBERG had claimed the possibility of using the blood groups in doubtful and disputed paternity cases, stating that knowing the groups of the children and of one parent, one could sometimes say what the other parent must be.

BUCHANAN strenuously objected to this, basing his objections mainly on several instances in which he found that parents, both of group I, had children of some other group. Should such instances become at all frequent, they might be cause for disturbance. BUCHANAN, however, showed such evident lack of knowledge of the fundamental principles of Mendelism, and of the Mendelian interpretation which had been given to the groups, that his objections do not assume a very serious aspect.

The possibilities, where parents, both of group I, have children of some other group, are, as pointed out by KEYNES (1921): (1) the observations are at fault; (2) the putative father is not the real father; (3) the Mendelian theory of inheritance is wrong. To these I would add a fourth, the possibility of more than four groups in human blood. This possibility will be considered later. KEYNES concluded that since the Mendelian theory of inheritance is so well established, and in general there is no reason for supposing that the observations are inaccurate, we are forced to the conclusion that in such a case the child is illegitimate. OTTENBERG answers BUCHANAN by saying that there is no reason for doubting the theory of Mendelian inheritance, and it is unlikely that BUCHANAN should have met with so many illegitimacies, so that his wrong conclusions must rest on his own mistakes.

To the support of a strict Mendelian interpretation of the blood groups have come other investigators. JERVELL (1923) in Christiania stated that he found the blood groups of 136 individuals in two generations of 32 Norwegian families to conform in every respect to the Mendelian interpretation. He concluded that a medico-legal application was thus possible. KEYNES (1921), in England, as before stated, upheld the Mendelian interpretation. He presented an exceptionally large pedigree: a family of fifty-nine persons in four generations, which bears out in every respect the results expected on a Mendelian basis. LATTES (1923), in Italy, confirmed the value of OTTENBERG'S theory of medico-legal application. WESZECZKY (1920) in Czechoslovakia, with families tested to the fourth generation, and TEBBUT and MCCONNEL (1922), in Australia, presented evidence to confirm the Mendelian interpretation of the groups. GICHNER (1922), in the United States, has pointed out BUCHANAN'S evident lack of grasp of the situation. The evidence is overwhelmingly in favor of a Mendelian interpretation. The only thing which may in the future indicate that the two points of view are not necessarily opposed is the recent claim that there really are more than two iso-agglutinins and two agglutinogens in human blood.

GUTHRIE and HUCK (1923) and HUCK and GUTHRIE (1924), present evidence to show that there are at least three iso-agglutinins and three agglutinogens in human blood, making twenty-seven biologically possible combinations. If the additional agglutinins are inherited in a manner similar to the others, eight groups would be formed. COCA and KLEIN (1923) found a third pair of iso-agglutination elements, which may be identical with those of GUTHRIE and HUCK. These, however, COCA and KLEIN showed not to be inherited as Mendelian allelomorphs. As yet

the possibility of more than four groups is an open question, but the inheritance of the four known groups is definitely Mendelian.

The medico-legal application, the possibility of which was mentioned by earlier writers (VON DUNGERN and HIRSCHFELD 1910, GIRAUD 1919, HIRSCHFELD and HIRSCHFELD 1919), but which was first clearly set forth by OTTENBERG (1921), is briefly as follows. Knowing the groups of the children and of one parent, it is sometimes possible to state what the other parent must be. The instances in which this can be done are tabulated in table 3. In other words, one can sometimes say that a child is *not* the offspring of certain parents; one can sometimes say that the child *might* be the offspring of certain parents; but one can never state that a child *is* the offspring of certain parents.

TABLE 3

Prediction of remaining parent groups. (*After* OTTENBERG).

KNOWN CHILDREN IN GROUP	ONE PARENT KNOWN TO BE IN GROUP	OTHER PARENT MUST BE IN GROUP
II	I	II or IV
II	III	II or IV
III	I	III or IV
III	II	III or IV
IV	I[4]	IV
IV	II	III or IV
IV	III	II or IV
II and III	I	IV
II and III	II	III or IV
II and III	III	II or IV
II and IV	I	IV
II and IV	II	III or IV
II and IV	III	II or IV
III and IV	I	IV
III and IV	II	III or IV
III and IV	III	II or IV

At various times it has been stated that the blood groups could be changed or modified by action of drugs or other agencies; a condition which might complicate the heredity of the groups; but the evidence now seems to show that the groups are remarkably stable. LEVINE and SEGALL (1922) reported that prolonged etherization might cause a tem-

porary change in the iso-agglutination phenomena. They cited instances to uphold this statement. HUCK and PEYTON (1923) tried experiments to test this and concluded that there is no change in the blood groups after ether anesthesia.

VORSCHÜTZ (1922) presented evidence that the previous taking of a drug, or general anesthesia, or Roentgen irradiation might modify the blood enough to change it from one group to another for the time being. HARPER and BYRON (1922) claimed that diet might influence agglutination. EDEN (1922) and DIEMER (1922) found changes in the iso-agglutinins after the administration of various drugs (quinine, calcium lactate, antipyrin, arsenic, ether, chloroform), and after exposure to Roentgen rays. MEYER and ZISKOVEN (1923) tested these claims, and found no such changes. They attributed the earlier results to a mistake due to sedimentation of corpuscles. MINO (1923) states from experiments with numerous patients and various drugs that it is impossible to modify the iso-agglutinins and to change blood grouping.

Another interesting phase of the problem is the question of blood groups in the new-born. The earlier workers discovered that the agglutinophilic capacity of the blood was usually present at birth, but that the specific iso-agglutinins might not appear until later. ROBERTSON, BROWN and SIMPSON (1921) confirmed these results experimentally, but stated that transfusion from mother to infant should not be made without first testing the compatibility of the blood. UNGER (1921) came to similar conclusions. HAPP (1920) found that both agglutinins and receptors might be absent at birth, but he also stated that compatibility tests should always be made. CHERRY and LANGROCK (1916) failed to find any agglutination whatsoever between the blood of a mother and that of her new-born babe. JONES (1921) found that the receptors were always present at birth, and that in most cases the iso-agglutinins were also present. He demonstrated iso-agglutinins in the blood of a seven-months fetus.

MCQUARRIE (1922) tested the blood of 180 new-born infants against the blood of their respective mothers. In nearly half there was no evidence of iso-agglutinins in the serum, nor of receptors in the red cells, of the infant. In 23 percent of the cases, however, the mother's serum agglutinated her infant's cells. DE BIASI (1923) found that in no case was there any agglutination between the blood of a mother and that of her new-born infant, regardless of whether or not they belonged to incompatible groups. Moreover, the cells of the infant always contained their full complement of receptors, since they could be easily grouped by means of test sera.

DE BIASI'S work would indicate that although the receptors were present in the red cells of the infant, the agglutinins of its own mother had no effect on them, and that a mother could safely be used as donor for her new-born infant without compatibility tests, thus confirming CHERRY and LANGROCK'S (1916) earlier work. The general opinion seems to be that the agglutinophilic capacity of the red cells is present at birth, although whether or not the cells in a new-born child can be agglutinated by the *mother's* serum is an open question. The specific iso-agglutinins may be delayed in their appearance for several months.

No definite physical characters of the blood are associated with the presence or absence of agglutinins, although ALEXANDER (1921), from a study of the blood groups of a number of cases, claimed that persons in groups I and III were peculiarly susceptible to malignant disease. BUCHANAN and HIGLY (1921), however, showed that no group was more susceptible than any other to disease. No human characters of any kind have been shown to be linked with the blood groups.

BLOOD-GROUP INHERITANCE IN ANIMALS

The other line of research on the inheritance of the groups, that of studying the behavior of the blood groups in animals, has not met with such success, chiefly due to the fact that no blood groups in animals have been clearly demonstrated.

VON DUNGERN (1910) sought to demonstrate by the absorption method that iso-agglutinins and agglutinogens were present in a variety of animals.

HEKTOEN (1907) made the first direct tests on animal blood. He used rabbits, guinea-pigs, dogs, horses and cattle. In no case did he find agglutination, although ten to twenty individuals of each species were used.

In 1911, OTTENBERG and FRIEDMAN studied rabbits and steers, and found that the bloods of thirty-two rabbits fell into four groups, while the bloods of eleven steers could be placed in three groups. To account for this, they assumed the presence in the blood of rabbits of two iso-agglutinins and two agglutinogens; in the blood of steers they assumed the presence of one of each.

INGEBRIGSTEN (1912 a, b) studied forty cats. In five cases he found inter-agglutination, but most instances showed no agglutination. He could not make a satisfactory grouping. In dogs he also failed to find iso-agglutinins.

In 1913, FISHBEIN studied several species, including 60 swine, 60 cattle, 40 sheep, 25 rabbits, 20 frogs and 10 dogs. He found only occasional agglutination. FISHBEIN concluded that iso-agglutination in animals

is a much less pronounced phenomenon than in man, and that no satisfactory grouping could be consistently made in animals.

OTTENBERG, FRIEDMAN and KALISKY (1913) found occasional agglutination, but no sharp grouping, in dogs. In 1915, OTTENBERG and THALHIMER confirmed INGEBRIGSTEN'S (1912 a, b) results that no grouping could be made in the blood of cats.

WESZECZKY (1920) found no agglutination in guinea-pigs, rabbits, cattle and chickens. In horses, swine and dogs he found occasional agglutination, but could make no grouping.

ROHDENBERG (1920) failed to find agglutination in fifty rats of different strains. MACDOWELL and HUBBARD (1922) did not find any agglutinins in mice, although ten widely different strains were used, involving 1180 combinations of serum and corpuscles.

PANNISSET and VERGE (1922) could not detect any evidence of fixed blood groups in either horses or cattle. PRZESMYCKI (1923) using the method of iso-transfusion, failed to find any evidence of agglutination in rabbits. In horses, however, the results indicated two groups. WALSH (1924) found irregular iso-hemagglutination in horses, but could not demonstrate any grouping.

The present writer (SNYDER 1924), studied rabbits for their iso-agglutinins. Practically every known variety of the domestic rabbit was used, the strains varying from the large Flemish Giant to the small Polish rabbit, and from stock which had been in American laboratories for generations to freshly imported animals. The rabbits were from Dr. CASTLE'S stock at the BUSSEY INSTITUTION, and the testing was done at the MASSACHUSETTS ANTITOXIN AND VACCINE LABORATORY. The technique was as follows: The rabbits were bled from the marginal ear vein. The skin over the vein was shaved and rubbed with xylol to induce hyperemia. A hot cloth was applied at the base of the ear. The blood was drawn through a 22-gauge needle into a 10-cc syringe.

Three drops of blood were added to 10 cc of sodium citrate solution (1-percent sodium citrate in isotonic salt solution). This gave a 2-percent suspension of blood without clotting. This suspension was centrifuged, and the supernatant fluid pipetted off. The original amount of solution was restored by adding isotonic salt solution.

The remaining portion of the blood taken from the rabbit was allowed to clot in a centrifuge tube. After an hour at room temperature, the clot was loosened. The tubes were allowed to stand overnight in the ice chest. The clot was then whirled down, and the serum was transferred

to a sterile vial. Sterile apparatus and rigid aseptic technique were used throughout the tests.

The macroscopic method of reading was used. Two-tenths cc of serum were added to one-tenth cc of washed corpuscles in small vials. The vials were then placed in the incubator at 37°C for an hour, after which the first reading was made. The vials were then placed in the ice-chest, and several subsequent readings made at intervals of an hour, and again after the vials had stood over night in the ice chest.

Each serum was tested against as many other corpuscles as possible. Its own corpuscles acted as a control. Serum from each strain was tested against corpuscles from each of the other strains.

Microscopic observations of hanging drops were made with about 10 percent of the combinations to act as a check. In every case the microscopic observation confirmed the macroscopic reading.

About two thousand combinations of serum and corpuscles were made, but no evidence of iso-agglutinins could be detected.

With regard to the agglutination of the cells of one species by the serum of another, some interesting results have been obtained. It has long been known that in general there was agglutination between the bloods of different species of animals (PFEIFFER 1904). Human cells appear to be constantly agglutinated by animal serum (MARX and EHRNROOTH 1904, WILLIAMS and PATTERSON 1910, KOLMER and MATSUMOTO 1920, KOLMER and TRIST 1920). HOOKER and ANDERSON (1921) were able to produce specific agglutinating sera for the four groups of human cells by immunization of rabbits.

Although in general the bloods of different species agglutinate each other, MACDOWELL and HUBBARD (1922) found that rat serum did not agglutinate mouse cells. WESZECZKY (1920) found that the serum of the buffalo (presumably *Bos bubalus*) did not agglutinate the cells of cattle. WALSH (1924) found that horse serum did not agglutinate ass cells, although in most cases ass serum agglutinated horse cells. Mule serum did not agglutinate either horse or ass cells, nor were mule cells agglutinated by horse or ass serum. Results such as these may be of taxonomic importance, and should be carefully followed up. Likewise agglutination tests on monkeys and the anthropoid apes should be made.

SUMMARY

1. The four known blood groups in human beings appear to be inherited on the basis of two pairs of Mendelian unit factors, the specific agglutinogens being dominant to their respective iso-agglutinins.

2. The recent claim that there are more than two iso-agglutinins and two agglutinogens in human blood, and therefore more groups, may in the future necessitate a modification of this scheme of inheritance.

3. On the basis of the facts known at present, a medico-legal application of the blood groups is possible.

4. The grouping can not easily be changed by the action of drugs, anesthesia, or Roentgen rays.

5. The agglutinogens are usually present at birth, but the specific iso-agglutinins may be delayed in their appearance for several months.

6. Blood groups are rare, if not entirely absent, in animals, and therefore no experimental method of studying their inheritance is readily available.

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MATERNAL INHERITANCE IN *BOMBYX MORI*[1]

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The term "maternal inheritance" implies a peculiar type of inheritance in which the external character of the offspring is governed by the genetic nature of the female parent. Though this mode of inheritance has hitherto been reported in various animals (sea-urchins, fishes, Limnaea) and plants (maize, soy-bean) (see MORGAN 1919, pp. 227–233; TERAO 1918), it has been most extensively studied in the silkworm moth, *Bombyx mori* L., by TOYAMA (1909, 1910, 1913). According to TOYAMA, the characters in the silkworm that are transmitted maternally are as follows:

Egg colors. Normal *versus* reddish brown, blue, certain albino, green and whitish gray.

Egg shapes. Normal *versus* spindle-shaped.

Yolk colors. Yellow *versus* white.

Voltinism or brood characters. Univoltine *versus* bivoltine.

As is well known, the egg-shell and yolk are produced in the maternal body before fertilization, and therefore belong to a different generation from the embryo contained in the same egg. This point was made clear by FEDERLEY (1914) in reference to TOYAMA'S work. Consequently, the egg-shapes that are dependent on the shell, exclusively, and the yolk colors, could not be called maternal in inheritance.

So-called "whitish gray" is the product of the normal color of the serous membrane seen through the characteristic milky-white egg-shell. As the shell character in question is quite independent from the serosa pigment, I have succeeded in my crossing experiments in combining the milky-white shell and the scarlet serosa, the result being a dilute red or pink color in external appearance.

The shell of the "blue" egg is opaque white in some degree, representing an intermediate character between the normal and "whitish gray." The serosa color of the blue egg is the same as that of the normal, but it appears "blue" as it is seen through the somewhat opaque white shell.

[1] Contributions from the Sericultural Laboratory, KYUSHU IMPERIAL UNIVERSITY, No. 2. This paper was read before the Biological Society of the Department of Agriculture on January 18, 1924.

The egg-shell of the green strains is tinted yellowish green, while it is colorless in the normal. This fact was known to TOYAMA, but he writes: "In Chinese, European, and in some green breeds, the green color of the shell may help the production of these green shades, but it is not the chief cause of the green color" (TOYAMA 1913, p. 381). We find considerable variation with regard to the green shade in eggs of the same batch as well as between different batches. To determine whether the green color is dependent on the shell color or not, I picked out the eggs with green shade from several batches during the period of hibernation, and classified them into five classes according to intensity of green color. They were put into an incubator, and the empty shell was observed after hatching of the larva. The result showed that the intensity of green color of the eggs before hatching is exactly proportional to that of the egg-shell observed when empty. Moreover, I have not been able to find any visible difference between the colors of the serous membrane in normal and green eggs. So we may safely conclude, I think, that the green color is exclusively due to the shell character.

In brown and white ("albino") eggs, on the contrary, the egg-shell is colorless, as is the case in the normal. Thus the term "maternal inheritance" should only be applied to the brown and white egg colors and to voltinism in its proper sense.

The characteristics of maternal inheritance as described in my Japanese books (TANAKA 1917, 1919), may be summed up as follows:

(1) F_1 individuals are like the female parent, regardless of the dominance or the recessiveness of her character.

(2) Dominant characters appear only in F_2.

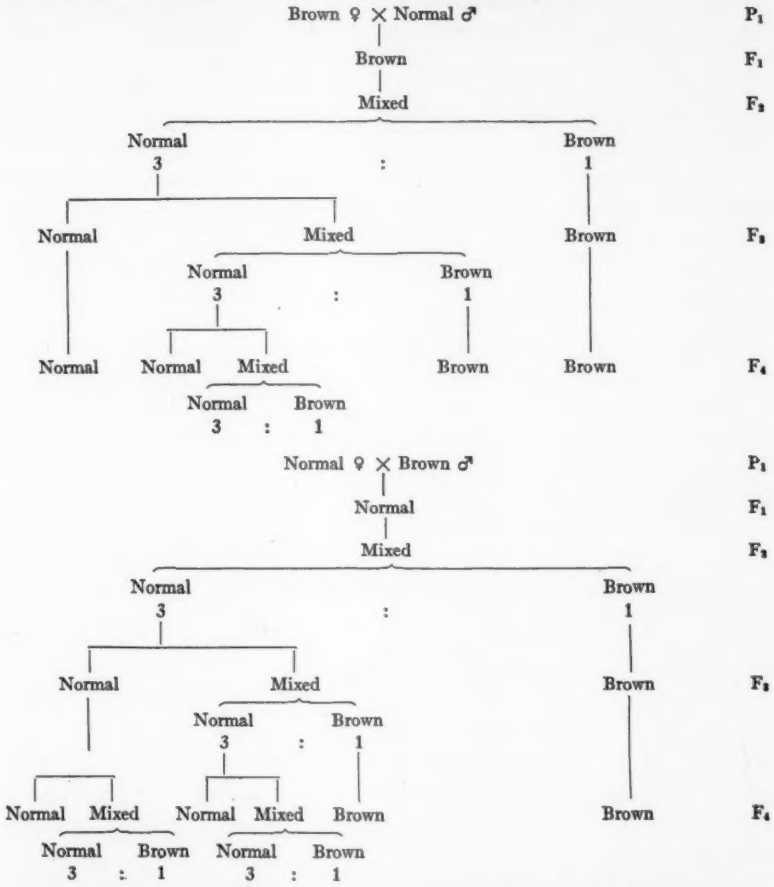
(3) Segregation occurs, apparently for the first time, in F_3, between different batches, but never in the same batch.

(4) Both the dominant and the recessive F_3 batches may, when inbred, give rise to both characters in the next generation.

I have repeated experiments similar to TOYAMA's and have got the same results. The only difference is that TOYAMA (1913, p. 393) gave the F_2 ratio as 2D : 1R, while it is evident, from my experimental results, that the ratio is actually 3D : 1R, as is theoretically expected.

WATANABE (1918, 1919) has established TOYAMA's conclusion on inheritance of voltinism by his extensive work with crosses between bivoltine and tetravoltine as well as between univoltine and tetravoltine races. His results are exactly comparable with those of the four characteristics of maternal inheritance mentioned above.

In the July number of "Genetics"[2] UDA (1923) reported a series of crossing experiments made between the normal and brown races, the results of which are summed up in the following diagrams:



UDA seems to believe that the occurrence of *mixed* batches is a normal phenomenon in maternal inheritance. TOYAMA, in certain cases, met with some mixed batches, but he says: "We shall discuss in our next paper the appearance of intermediate or mixed batches in certain line- or cross-breedings, a fact which seems to be *inconsistent* with maternal inheritance"

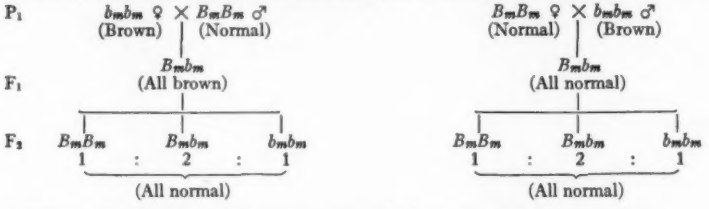
[2] This issue of "Genetics" reached me on December 25, 1923.

(TOYAMA 1913, p. 399). But his "next paper" has not appeared because of his untimely death.

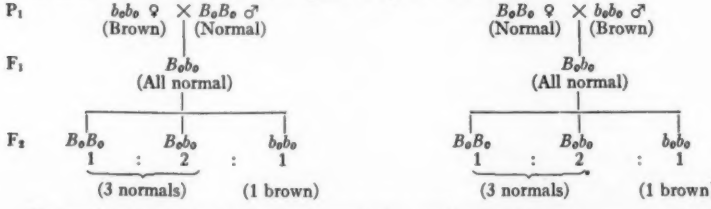
UDA's results are very perplexing. So far as F_1 colors are concerned the inheritance is typically maternal, while in F_2 and in later generations it is like ordinary inheritance. The hypothesis of "time of action" does not, it appears to me, afford any clue to an explanation of these facts. Some other difficulties are encountered in the back-crossing experiments shown in his plate 1 (UDA 1923, p. 330, lots 12, 13, 14, 16, 17, etc.) which UDA does not try to analyze.

His results may easily be accounted for, however, if we assume two brown factors, one of which is maternally and the other ordinarily inherited. Let us represent the maternal brown gene by b_m, its normal allelomorph by B_m, the ordinary brown gene by b_o, and its normal allelomorph by B_o. Let us consider, in the first place, the two genetic pairs, separately, and then simultaneously.

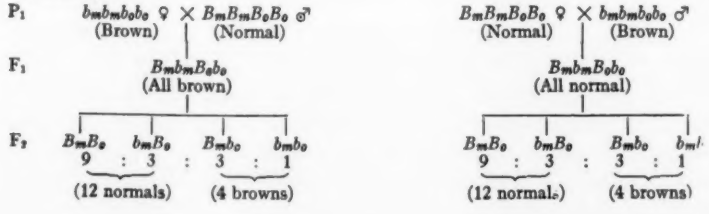
First, when the maternal brown gene is solely concerned:



When the ordinary brown gene only is concerned:



Second, when the maternal and the ordinary brown genes act simultaneously:



Thus, F_1 eggs always resemble the mother in virtue of the maternal factors b_m and B_m, while each F_2 batch consists of 75 percent normals and 25 percent browns, the latter form owing its appearance to the ordinary brown factor b_o. The F_2 brown eggs, being produced by individuals homozygous for b_o gene, will produce no normal offspring when the parents have been mated *inter se*. These points are exactly realized in UDA's experiments.

Among individuals derived from F_2 normal eggs, we may expect six different genotypes in the following ratio:

1	$B_mB_mB_oB_o$	4	$B_mb_mB_ob_o$
2	$B_mb_mB_oB_o$	1	$b_mb_mB_oB_o$
2	$B_mB_mB_ob_o$	2	$b_mb_mB_ob_o$

As the gametic ratios will be the same in both sexes, the F_3 eggs must be produced by random matings of these genotypes in the ratio given above. Thus, there will be three classes of F_3 batches: The first class will consist of normal eggs only, the second class of brown eggs only, and the third class of normal and brown mixed in a 3 : 1 ratio. The theoretical frequency of each class is 60, 36 and 48, respectively, i.e., a 5 : 3 : 4 ratio.

As UDA does not give the actual numbers of normal batches and mixed ones in F_3 or in any other generation, we cannot decide whether the frequency calculated above was realized or not. The brown batches, smallest in number, were possibly discarded as unfertilized eggs by the author who did not expect their occurrence.

The results of back-crossing also favor my supposition. An F_1 male gave, on mating to a pure brown female, only brown eggs as expected (UDA 1923, p. 330). Some of these F_2 browns, mated *inter se*, produced only brown eggs, some other individuals deposited normal and brown eggs in a 3 : 1 ratio (lot 12), and still others gave the two colors in a 1 : 1 ratio (lot 13). If only the maternal genes were concerned, the F_3 generation should have consisted of normal and brown batches in equal numbers, but no mixed batches were expected. If we assume, on the contrary, that only the non-maternal gene was responsible for the brown color in question, the F_2 batches ought to have been all mixed ones (in a 1 : 1 ratio), while the F_3 consisted of mixed batches (in a 3 : 1 ratio) and brown ones, but no mixed batches in a 1 : 1 ratio were seen to occur.

The difficulties mentioned above may, as shown below, easily be solved on the assumption of two allelomorphic pairs as already noted. In a cross between a pure brown ($b_mb_mb_ob_o$) female and an F_1 ($B_mb_mB_ob_o$) male, four different genotypes, namely, $B_mb_mB_ob_o$, $b_mb_mB_ob_o$, $B_mb_m\ b_ob_o$ and $b_mb_mb_ob_o$ will be produced in 1 : 1 : 1 : 1 ratio in the same batch. The F_2 eggs are,

regardless of their different genetic nature, all brown in external appearance. As the four genotypes given above should theoretically occur in equal numbers in both sexes, the following sixteen combinations will be expected in producing the F_3 eggs.

F_2 ♀ × ♂	F_3 eggs
$B_mb_mB_ob_o \times B_mb_mB_ob_o$	9 B_mB_o : 3 b_mB_o : 3 B_mb_o : 1 b_mb_o 12 normals 4 browns
$B_mb_mB_ob_o \times b_mb_mB_ob_o$	3 B_mB_o : 3 b_mB_o : 1 B_mb_o : 1 b_mb_o 6 normals 2 browns
$B_mb_mB_ob_o \times B_mb_mb_ob_o$	3 B_mB_o : 1 b_mB_o : 3 B_mb_o : 1 b_mb_o 4 normals 4 browns
$B_mb_mB_ob_o \times b_mb_mb_ob_o$	1 B_mB_o : 1 B_mb_o : 1 B_mb_o : 1 b_mb_o 2 normals 2 browns
$b_mb_mB_ob_o \times B_mb_mB_ob_o$	3 B_mB_o : 3b_mB_o : 1 B_mb_o : 1 b_mb_o All browns
$b_mb_mB_ob_o \times b_mb_mB_ob_o$	3 b_mB_o : 1 b_mb_o All browns
$b_mb_mB_ob_o \times B_mb_mb_ob_o$	1 B_mB_o : 1 b_mB_o : 1 B_mb_o : 1 b_mb_o All browns
$b_mb_mB_ob_o \times b_mb_mb_ob_o$	1 b_mB_o : 1 b_mb_o All browns
$B_mb_mb_ob_o \times B_mb_mB_ob_o$	3 B_mB_o : 1 b_mB_o : 3 B_mb_o : 1 b_mb_o 4 normals 4 browns
$B_mb_mb_ob_o \times b_mb_mB_ob_o$	1 B_mB_o : 1 b_mB_o : 1 B_mb_o : 1 b_mb_o 2 normals 2 browns
$B_mb_mb_ob_o \times B_mb_mb_ob_o$	3 B_mb_o : 1 b_mb_o All browns
$B_mb_mb_ob_o \times b_mb_mb_ob_o$	1 B_mb_o : 1 b_mb_o All browns
$b_mb_mb_ob_o \times B_mb_mB_ob_o$	1 B_mb_o : 1b_mB_o : 1 B_mb_o : 1 b_mb_o All browns
$b_mb_mb_ob_o \times b_mb_mB_ob_o$	1 b_mB_o : 1 b_mb_o All browns
$b_mb_mb_ob_o \times B_mb_mb_ob_o$	1 B_mb_o : 1 b_mb_o All browns
$b_mb_mb_ob_o \times b_mb_mb_ob_o$	All b_mb_o All browns

Thus we may expect three classes of F_3 egg-batches: (1) those with brown eggs only; (2) those with normal and brown eggs mixed in 3 : 1 ratio; (3) those with normals and browns mixed in equality. These three classes were all realized in UDA's experiments.

Similar cases are also found in lots 16, 17, 22, 23, etc. (UDA 1923, p. 330), which may be explained in the same way as above, otherwise they seem very difficult to analyze.

According to UDA, F_1 brown eggs are quite the same in color as the eggs of the brown mother, while F_2 browns are of a different tint from the original brown. This is explained by the assumption that the maternal gene (b_m) gives rise to a light brown color, while the ordinary brown gene (b_o) gives rise to a dark brown; the double-recessive ($b_m b_m b_o b_o$) eggs are light-colored because the light brown is dominant to dark brown. Thus F_1 eggs ($B_m b_m B_o b_o$) from the cross between brown female ($b_m b_m b_o b_o$) and normal male ($B_m B_m B_o B_o$) are brown because of the maternal brown gene b_m; therefore, they show exactly the same color as their mother, while the F_2 brown eggs ($B_m b_o$ and $b_m b_o$) owe their brown color to the ordinary brown gene, b_o, so that they are dark brown.

It may be interesting to note that UDA's brown strain had descended from that of TOYAMA, as UDA states in his paper. TOYAMA also described, as already mentioned, the occurrence of some mixed batches, which is an indication of the continuation of both b_m and b_o genes since his time. He considered, however, the occurrence of mixed batches an inconsistent phenomenon from the point of view of maternal inheritance.

I have some brown strains of apparently different origin from that of TOYAMA and UDA. One of them we call "waxy brown" and have found it to be inherited as an ordinary recessive to normal. The other brown strain proved itself to be maternal in inheritance. If these two different brown genes were combined in the same individual, and crossed to normal reciprocally, the results would, perhaps, be identical with those obtained by UDA.

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LINKAGE OF ALBINO ALLELOMORPHS IN RATS AND MICE[1]

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Present concepts of some phenomena of inheritance, derived from experimental studies of unit characters, are definite enough to allow certain predictions to be made with considerable accuracy. Of the genetic linkage or partial coupling of characters there exist some remarkable examples. It has been established, for instance in Drosophila, that when two pairs of characters show a given degree of linkage, any allelomorph of either will show a similar linkage with the other pair. However, heretofore, no material has been available to enable us to know whether this generalization is tenable in mammals. It is important, therefore, to make use of the first opportunity to test this point.

In the Norway rat and house mouse the linkages have been determined between the characters, albinism and pink-eye with colored coat. These characters are similar in both forms. Both characters are recessive. Albinos in both rat and mouse are devoid of pigment in eye and coat, but pink-eyed individuals develop traces of black pigment in the eye and coat and the full amount of yellow pigment in the coat, so far as their constitution in other genes permits. Recently, two dilute (colored) allelomorphs of albinism have been described for the mouse by DETLEFSEN (1921) and FELDMAN (1922), and one for the rat by WHITING and KING (1918). These allelomorphs of albinism have parallels in the rabbit, guinea-pig, and probably other forms.

The most outstanding characteristic of the albino allelomorphs is a practical elimination of the yellow pigment from the coat. In addition, a progressive decrease in the intensity of black and brown is obvious, as one proceeds from the intense to the dilute members. The extremities of the animal, the ears, eyes, nose, and tail region, are affected less than the other regions. The effects produced by these allelomorphs persist when they are in conjunction with other dilution factors. For example, rats and mice homozygous for pink-eye as well as for an albino allelomorph,

[1] This work on mice was begun at the Genetics Laboratory of the UNIVERSITY OF ILLINOIS, and completed at the Bussey Institution of HARVARD UNIVERSITY. The work on rats was done entirely at the latter institution.

possess little or no pigment, much less than pink-eye alone would produce. Normal color is completely dominant over the other members of the albino series in the rat and mouse, and intermediate members are incompletely dominant over each other and over albinism.

This paper deals with the more intense allelomorph in the mouse described by the writer (FELDMAN 1922), and the one described for the rat by WHITING and KING (1918). For convenience these two factors will be spoken of as ruby-eyed dilution (from the effects produced on the pigment of the eye) and will be designated by c^r, indicating that they are allelomorphic to color, C, and complete albinism, c. The pink-eye factor will be designated by p; its allelomorph, dark-eye, by P.

The method of procedure in determining the occurrence and strength of linkage was essentially the same in both rats and mice. In the former, pink-eyed colored animals, $CCpp$, were mated with ruby-eyed dilute, c^rc^rPP. In mice the same cross was made; and in addition, ruby-eyed dilute (c^rc^rPP) animals were mated to albinos carrying the pink-eye factor, $ccpp$. In both cases the F_1 animals, heterozygous for the two factor-pairs concerned, were mated to homozygous double-recessives, $ccpp$. Briefly, from the first type of cross (repulsion), the F_1 animals may be expected to produce gametes of the classes, Cp, c^rP, CP and c^rp. Of these, the last two are the crossovers. And from the second cross (coupling), we expect gametes from the F_1 mice as follows; c^rP, cp, c^rp and cP. In this case, also, the last two are crossover classes.

By observing the progeny of the F_1 animals when mated with double-recessive animals, it was possible to determine the proportion of each of the four kinds of gametes produced by the F_1 individuals. An exception existed in the mouse cross involving albinism. In this case, only one class, the dark-eyed non-crossover (c^rP), is distinguishable from the others. It was necessary to calculate the percentage of crossover gametes by assuming that the indistinguishable non-crossover class, cp, tended to equal the observed non-crossover class, and therefore that the remaining gametes which functioned, composed the two crossover classes. Where the error of sampling is not large, this should not injure the reliability of the results.

As a means of increasing the tests on individual F_1 rats, their progeny were classified at birth and discarded. At that age one crossover class, namely, the double-dominant, dark-eyed animals, CP, can be easily distinguished from the others. It is reasonable to assume that the other crossover class, c^rp, will tend to be of equal size, and that the total crossing over may be obtained by doubling the observed. The use of this method

increases the probable error on crossover percentages considerably, as compared with the direct classification of all types.[2] Because of this fact, small samples of gametes, as individual tests, are discussed solely in terms of the known, dark-eyed class. However, there is justification for concluding that the observations on that class are valid in regard to the reciprocal class, and therefore to the total crossovers.

Table 1 gives a summary of my data with those of CASTLE and WACHTER (1924) from their comparable experiments in which the linkage between albinism and pink-eye was studied. They found the percentage of crossing over between albinism and pink-eye in the rat to be 19.66 ± 0.26, while

TABLE 1

Summary of data on the linkage between pink-eye and ruby-eye (or its allelomorph, albinism) in rats and mice

GENES CONCERNED	SEX OF F_1 PARENT	GAMETES TESTED	CROSSOVER GAMETES	PERCENT CROSSOVERS	NATURE OF CROSS
Ruby-eye and pink-eye in rats	Female	3,075	492	16.00 ± 0.86	Repulsion
	Male	2,742	508	18.52 ± 0.91	Repulsion
Total		5,817	1000	17.18 ± 0.62	
Albinism and pink-eye in rats	Female	11,480	2,518	21.93 ± 0.44	Repulsion
	Male	21,255	3,920	18.39 ± 0.32	Repulsion
Total		32,735	6,438	19.66 ± 0.26	
Ruby-eye and pink-eye in mice	Female	313	51	16.29 ± 1.91	Repulsion
	Male	275	32	11.64 ± 2.03	Repulsion
	Female	1,040	208	20.00 ± 1.48	Coupling
	Male	129	15	11.63 ± 4.18	Coupling
Total		1,757	306	17.42 ± 1.14	
Albinism and pink-eye in mice	Female	3,345	550	16.44 ± 0.82	Repulsion and coupling
	Male	7,057	965	13.77 ± 0.57	
Total		10,352	1,515	14.63 ± 0.47	

[2] The method of calculating probable errors used by CASTLE and WACHTER (1924) was applied by the author here. That is, n represents one-half instead of the whole sample, and the values of P. E. have been taken from EMERSON'S tables.

I found the crossover percentage to be 17.18 ± 0.62 between ruby-eye and pink-eye. In the mouse experiments involving albinism, those workers found 14.63 ± 0.47 percent crossing over, and in the experiments involving ruby-eye I found the crossover percentage to be 17.42 ± 1.14. The numbers secured by CASTLE and WACHTER probably give an accurate idea of what the crossover percentage is, between the two genes in question. The same is true of my data concerning ruby-eye and pink-eye, with more reservation, however, because of the smaller numbers which I recorded. Further, the differences between our figures in either species are not statistically significant. The results obtained in these experiments warrant the conclusion, therefore, that the ruby-eye allelomorph of albinism has the same linkage strength with pink-eye that albinism has, in both the rat and mouse.

In their experiments dealing with linkage in rats and mice, CASTLE (1919), DUNN (1920), and CASTLE and WACHTER (1924) have secured results which indicate a significant difference between the crossover percentage exhibited by ova and that exhibited by spermatozoa in the same cross. Their data show in every instance, a higher percentage of crossing over among the gametes of F_1 females than among those of F_1 males. In order to learn what my data yield on this point, the sexes have been tabulated separately (see table 1). In both of my crosses in mice, crossing over was higher in females than in males, which agrees with the results obtained by CASTLE and others. However, in my work on rats, the opposite obtains; females yielded 16.00 ± 0.86 percent, while the males gave 18.52 ± 0.91 percent.

However, it does not appear safe to assume that an exception to the general situation has been found. The crossing over for the two sexes is not so widely different as to lead to the conclusion that the apparent reversal, which my rat data show, would persist, if the sample of gametes examined was increased sufficiently. The occurrence of a sample such as I secured, precludes the possibility, however, of a large general excess of crossing over in the female over that in the male.

Figure 1 shows the variation among individual F_1 rats in the percent of the dark-eyed class, *CP*, among their gametes. The range is from 0.0 to 28.6 percent. The mean variate is 8.9 percent of dark-eye; the standard deviation is 5.21 percent. The variation can be readily ascribed to chance sampling, since the average number of gametes per rat was only 41.26. It may be noted that the males (indicated by the broken line) have essentially the same distribution as the females, which are included with the males in the total shown by the unbroken line.

In addition to the above tabulation, the individual records have been arranged according to the parentage of the animals. This was undertaken in an effort to discover whether there was a tendency among any of the original parental rats, to produce F_1's whose crossing over was outstandingly either high or low; for such a tendency would indicate at once the presence of genetic modifiers of crossing over. A careful examination of the data when they were thus arranged, failed, however, to disclose any evidence of the presence of such genetic factors.

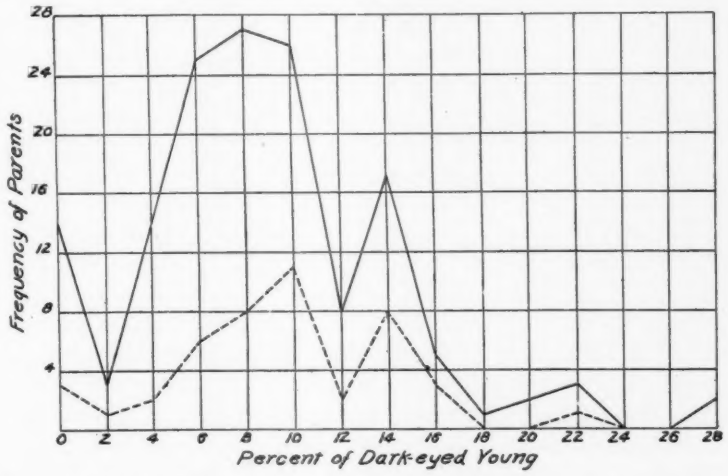

FIGURE 1.—Variation in percentage of the dark-eyed class, *CP*, among the gametes of individual F_1 rats. The unbroken line represents both females and males; the broken line, males only.

SUMMARY

1. The albino allelomorphs in the rat and mouse have the same linkage relation with the character pink-eye, that albinism has.

2. There is probably a small but significant difference between the sexes in rats and mice in crossing over. It is higher in the female than in the male.

3. Rats have a normal frequency distribution as regards the amount of crossing over among their gametes.

4. Linkage in F_1 rats does not appear to be influenced by genetic factors received from their parents.

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